

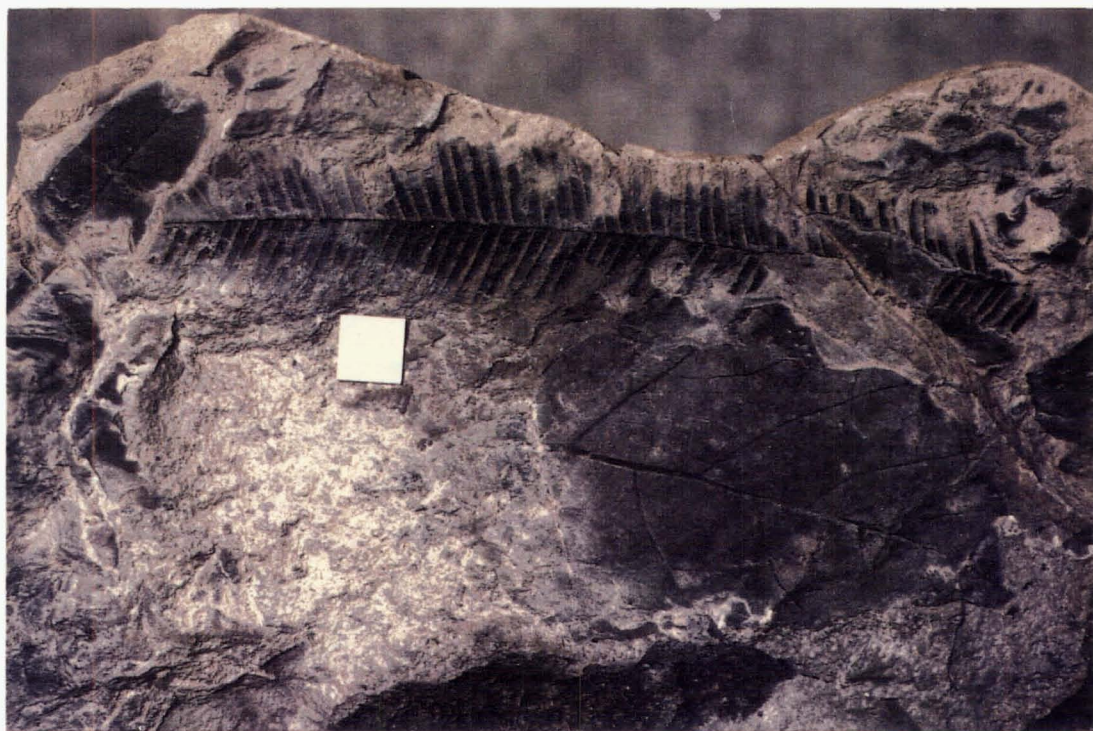
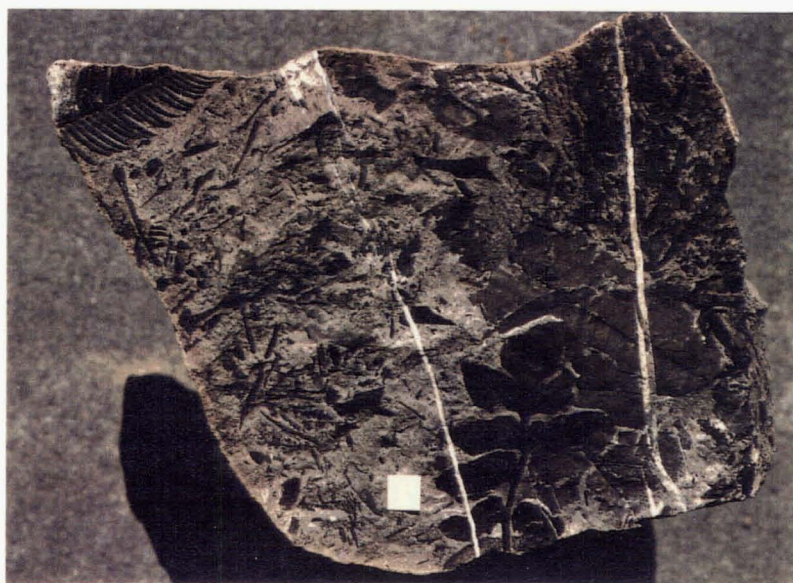
**TAXONOMIC INVESTIGATION OF ELEMENTS FROM THE
EARLY CRETACEOUS MEGAFLORA FROM THE MIDDLE CLARENCE
VALLEY,
NEW ZEALAND**

A thesis
submitted in partial fulfilment
of the requirements
of the degree of
Doctor of Philosophy
in Palaeobotany
in the
University of Canterbury

by
Ian L. Daniel

University of Canterbury
1989

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FRONTISPIECE

Above: *Ptilophyllum seymouricum*, *Thinnfeldia* sp., *Proteaceophyllum irregulare*, 522.30b.

Below: *Ptilophyllum seymouricum*, *Proteaceophyllum irregulare* (top left), *Latifolium parvilobum* (centre), 522.77a.

TAXONOMIC INVESTIGATION OF ELEMENTS FROM THE EARLY CRETACEOUS MEGAFLORA FROM THE MIDDLE CLARENCE VALLEY, NEW ZEALAND.

Abstract

The fossil megaflora of the middle Clarence valley, South Island, New Zealand, contains leaf forms attributable to all the following plant groups: liverworts, ferns, equisetaleans, cycads, bennettites, pentoxylaleans, ginkgoaleans, araucariaceans, podocarps, pteridosperms and dicotyledons. The elements investigated here are taxa belonging to *Phyllopteroides*, *Taeniopteris*, Cycadales, Bennettitales, *Ginkgo*, *Agathis* and dicotyledonous foliage form species.

The sediments in which this megaflora occurs are fluviatile and lacustrine and were laid down in a coastal region of South Gondwana. The age of the deposits is late Albian/early Cenomanian. The palaeolatitude was high, being within the Antarctic Circle. Palaeoclimatic evidence shows that the climate of polar regions in Cretaceous times was mild temperate and highly equable at least in coastal regions.

Methods of extraction and photography of fossil cuticle are described. Numerical taxonomic methods are used to analyse 1) the relationships of fossil taxa within particular plant groups, 2) between New Zealand and Australian fossils, and 3) between a fossil species and extant species of *Agathis*. The new term numerotype is here proposed to rationalise variation of characters within a taxon for computational purposes.

Thirty-four new leaf form species are described systematically, of which 22 are dicotyledonous. These dicotyledonous leaves are all simple, broadly laminate, pinnately reticulate-veined and petiolate, and possibly some were deciduous.

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Explanation to Plates

For simplicity, the prefix CU and suffix Cl of collections held at the University of Canterbury have been omitted from the legends to the plates.

Plates 5-9 show some of the blocks in the collection. Overlays indicate the # number of certain leaves. They are provided to identify individual leaves, not taxa.

The white square used as a scale in most of the macrophotos is one centimetre square.

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CHAPTER 1. INTRODUCTION

1.1. Composition of the Clarence palaeomegaf flora

The plant megafossils which form the basic material for this thesis occur in terrestrial sediments in the middle Clarence valley between the Seaward and Inland Kaikoura Mountains, South Island, New Zealand (Fig.1). Their existence was first reported by Alexander McKay in 1886. The only relatively recent publication which includes elements of the flora is that of McQueen (1956) who described some pteridophyte and cycadophyte taxa. Otherwise, the flora remains entirely undescribed even though its existence has been known for a century.

The diverse flora contains leaf forms attributable to all of the following (Plates 5-35): liverworts, (both leafy and thallose), ferns (including four spp. of *Phyllopteroides*), *Equisetum* sp., cycads (two spp. of *Nilsson*), bennettites (one sp. of *Nilssoniopteris*, one sp. of *Otozamites*, one sp. of *Ptilophyllum*, one sp. of *Anomozamites*, five spp. of *Pterophyllum*), a pentoxylalean sp., a *Ginkgo* sp., araucariaceans (two spp. of *Agathis* as well as species of *Araucaria* sect. *Eutacta* and *A.* sect. *Columbea*), many species of podocarps, and pteridosperms, (represented by the form genus *Thinnfeldia*, most likely to be a corystosperm), as well as angiosperm leaves. Several fructifications and seeds of as yet unknown affinities have also been found. The angiosperm leaves are all dicotyledonous and approximately equal the collective gymnosperm content in abundance. The sole angiospermous floral part so far found is a magnoliid tepal which is referred to *Archaeopetala* Dilcher and Crane (1984).

To date, some 60 different plant taxa have been described or provisionally identified (see Appendix 5). Only species belonging to *Phyllopteroides*, *Taeniopteris*, Cycadales, Bennettitales, Pentoxylales, *Ginkgo*, *Agathis* and Angiospermae have yet been investigated taxonomically in this study.

This Early Cretaceous angiosperm megaf flora assemblage appears to be unique in the Southern Hemisphere. More widely-known New Zealand Cretaceous megaf floras, e.g. Shag Point, Pakawau, are of Late Cretaceous (Senonian) age. The only extensive study of these was carried out by Ettingshausen (1887,1891) on a collection sent to him in Vienna. A sequence of Australian deposits ranging from lower Neocomian to Albian in age appears, despite an earlier report to the contrary (Douglas, 1969), to be

quite devoid of angiosperms. Cretaceous rocks are altogether poorly represented in southern Africa (Anderson & Anderson, 1985, p.53). A deposit of Aptian age in Argentina (Romero & Archangelsky, 1986) has provided only one leaf form sufficiently well preserved to permit description.

Reviews of Late Cretaceous and Cenozoic vegetation changes by Mildenhall (1980) and of the history of palaeobotanical investigations in New Zealand by Raine and Pocknall (1983) indicate that, apart from studies of isolated taxa, there have been few modern studies of New Zealand post-Jurassic palaeomegaf flora. All have been of Tertiary age. Oliver described Pliocene leaves from the Waipaoa Series at Ormond (Oliver 1928) and ?Upper Miocene leaves from Kaikorai Valley, Dunedin (Oliver 1936). McQueen (1954) revised Oliver's Ormond flora and described new species from other Plio-Pleistocene sites from the Wanganui Series. Holden (1982a,b) described Miocene leaves from the Longford Formation in the Murchison area.

1.2. History of previous studies of the middle Clarence valley

When Alexander McKay travelled through the Clarence valley in January and March of 1885 in the course of a geological survey of southern Marlborough, he collected fossil leaves from the coal-bearing beds at Red Hill Stream, Quail Flat and Seymour Stream. He reported (McKay 1886, pp.27-28 & 98-104) the occurrence of "dicotyledonous leaves, abundance of a long narrow leaf with parallel venation, and four or five species of fern" from Red Hill Stream. The "ferns" included *Taeniopteris* and a plant which "closely resembles *Danaeopsis* and *Sphenophyllum* of the Triassic and Jurassic beds of India". From the "southern end of Quail Flat" he reported a "very large dicotyledonous leaf, with *Dammara* leaves, *Taeniopteris*, etc ... Casts of trees 18 in. to 2 ft. in diameter ... and *Polypodium*(?)". "*Taeniopteris* and dicotyledonous leaves of large size and finely preserved were obtained" from the "upper end of Quail Flat".

McKay's report included sketches of geological sections. One of these (loc.cit.p.101), cf. Plate 3A, "across the Clarence River at crossing to Quail Flat" shows a terrace cut in "coal beds". He comments "Fossil plants are abundant in the beds immediately associated with the coal-seams; but, there being more convenient localities for collecting from the same horizon on the south-east bank of the river

at Quail Flat, no collection was made from this section". During the present study, fossil leaves have been collected from these beds and it is proposed this terrace be named "Alexander McKay Terrace" in his honour.

At an earlier date (during 1867) John Buchanan had explored the area between Cape Campbell and Motunau making various fossil collections and travelling inland at the Awatere River and Seaward Kaikoura Range. In his abstract report accompanying Buchanan's "Exploration Report on the Kaikoura District", James Hector (1868, p. 17) lists the formations present, including under Cretaceo-Tertiary "Ferruginous clays, with septaria, containing upper secondary fossils (the Amuri beds)" and "Sandstone and grit with plants, representing the West Coast Coal Fields, are present probably at Motunau".

In an abstract (Hector 1878) of a work "On the Fossil Flora of New Zealand" which was never published but for which plates were prepared (see Section 1.6), Hector states (p. 536) "The Neocomian strata (or Amuri series) which are so rich in the remains of fossil reptilia, are interesting from their affording the earliest specimens of a true Dicotyledonous leaf, associated with the foliage of *Dammara* and *Araucaria*". There is no indication of exact locality(ies) and it is furthermore unclear precisely to which horizons Hector was referring as the stratigraphy he embraced changed with time. However it is fairly certain that neither Buchanan in 1867 nor McKay during his earlier visits to the Kaikoura area in 1873 and 1876 penetrated the middle Clarence valley area, in which case Hector must have been referring to plant fossils collected from elsewhere in the Kaikoura region, possibly from the vicinity of the Haumuri Bluff. If so, he was referring to a horizon which has not yet been rediscovered. It seems that sight has also been lost of the specimens themselves.

Hector (1886a) made use of four of McKay's Clarence fossils in a display of New Zealand fossils for the Indian and Colonial Exhibition in London in 1886 but did not include figures of them in his "Outline of New Zealand Geology" (Hector 1886b).

These leaf and wood fossils otherwise received scant attention from palaeobotanists for nearly seventy years. Unfortunately a collection of New Zealand Cretaceous and Tertiary leaf fossils had already, in 1884, been sent by Hector to Baron C. von Ettingshausen in Vienna. Thus the Clarence valley specimens did not come to Ettingshausen's attention. Hector did however refer to the Clarence collections in a footnote (p. 242) to Juhl's translation of Ettingshausen's 1887 paper (Ettingshausen 1891).

J. Allan Thomson (1913, p.17) made specific mention of the plant beds at "Amuri Bluff, the Malvern Hills, the Clarence Valley, and Shag Point" and indicated that his namesake, G.M. Thomson, had "commenced the formation of a series of nature prints of the leaves of the older elements of the New Zealand flora", to allow the correlation of the plant fossil beds of the main coalfields. In a footnote (*loc. cit.*) he also indicated that Professor Marshall of Otago University was to commence the study of the leaf fossils. Regrettably neither of these projects were subsequently to come to fruition. Stopes (1914) described araucariacean wood from Haumuri Bluff. Arber (1917), in his studies of New Zealand Mesozoic plants, examined only fossils of the earlier Mesozoic periods, i.e. those of Triassic and Jurassic age.

J.A. Thomson was the first geologist after McKay to visit Quail Flat (in 1912). However, his reports (1917, 1919) refer only to the plant fossils mentioned by McKay. In 1953, field-work for a revision of the geology of the area was carried out by a party led by H.E. Fyfe. Two reports resulted from this survey; a description of pteridophytes and cycadophytes by McQueen (1956) and an account of the geology by Suggate (1958). Recently (1978-79) M.B.Reay carried out a reappraisal of the geology of the area (Reay 1980, 1987 and in prep.). He reported (Reay 1980, p.68) the microfloral content of the Warder Coal Measures as determined by J.I.Raine, N.Z.G.S. in preliminary palynological studies. It is understood that these studies are continuing. He brought megafossil localities to the attention of J.D.Lovis; in particular, boulders at Horse Flat. The collections made then, together with those made in 1984-87 by I.L.D. and J.D.Lovis, involving the accumulation of more than one thousand collection numbers, has now produced evidence of what is arguably New Zealand's richest Mesozoic megaf flora.

1.3. Sediments

The sediments in which the fossils occur are fluvatile and lacustrine. The majority of the fluvatile beds consist of finely laminated mudstones (Plate 4) with coaly layers of overlapping, locally-derived leaves, interspersed with sandstone lenses (crevasse ^(see Addenda)splays) (Plate 3C,D), containing dispersed leaves and woody fragments transported from the hinterland. This type of sequence is interpreted as being the river bottoms of a large river bordered by levees and back swamps. Deposits away from the

main river valley are thinly bedded mudstones and palaeosols (Plate 2B), or lacustrine sandstones. The former yield poor fossils, the latter well-preserved, locally-derived leaves. One locality has beds of cross-bedded sandstones (Plate 1B,C) with coarsely preserved fossils. The sandstones are overlain by tuffs with very finely preserved leaves. The tuffs are in turn overlain by several flows of basaltic lava.

The area of deposition was in the southern coastal region of Gondwana. Palaeomagnetic data from Mount Somers (Oliver et. al., 1979) and Buller Gorge (Grindley and Oliver, 1979), together with recent palaeogeographic reconstructions (Dr. J. Bradshaw, pers. comm., 1987), indicate that the palaeolatitude of the area may have been as high as 80°S. Certainly it was well within the Antarctic Circle.

1.4. Age of the deposits

The age of the beds containing plant fossils was given by McKay as Cretaceous. Thomson (1917) included them in his Clarentian Group, fossils from which were correlated by Woods (1917) with the Lower Utatur of India and hence with the Gault and Upper Greensand (= Albian) of England. Findlay & Marwick (1940,p.84) suggested that the Clarentian should be tentatively regarded as covering the period Albian to Coniacian on the basis of the fossils then known. Later (1947,p.229) they raised the status of Thomson's Clarentian Group to Clarence Series but no stages were proposed. Wellman (1955,p.93-118) restricted the term Clarence Series to the fossil beds known to Thomson in the type area and later (Wellman,1957) proposed four stages (Coverian, Urutawan, Motuan and Ngaterian) within the series, which he correlated with Albian to Turonian time. Subsequently, Hall (1963) abandoned the Coverian as a separate stage. McQueen (1956,p.675) suggested that the plant fossils present, and the position of the "coal measures conformably underlying marine sediments containing...[zone fossils]..." indicated that "The Seymour River coal measures are thus either basal Senonian or probably Turonian" and classed them as ?Turonian. However, Douglas and Williams (1982,p.178) suggest that the pteridophytes and cycadophytes described by McQueen (1956) "indicate affinities with Victorian Zone B [Neocomian] or Zone C [Aptian]". Suggate (1958) included the coal measures, the overlying volcanics, and coarser grained plant-bearing sediments which overlie the volcanics all within his Gridiron

Formation. Suggate postulated a Ngaterian (Albian-Cenomanian) age for the Gridiron Formation, based on its stratigraphic position between more precisely dateable (on macrofauna) sediments.

Lensen (1978) gave the name Warder Coal Measures to the beds underlying the basalt flows of the Gridiron Formation which he equated with the Lookout Volcanics of the Awatere valley to the northwest. The coarser grained plant-bearing beds which overlie the volcanics are named Willows Member by Reay (1980, and in prep.). This latter unit outcrops at the locality identified by McKay (1886) as the "upper end of Quail Flat".

A recent development has been the clarification of zonation of the Australian Early Cretaceous megafloras by means of *Phyllopteroides*, an osmundaceous fern (Cantrill and Webb, 1987). A preliminary study (see Chapter 4) of *Phyllopteroides* specimens in the Clarence flora indicates that a parallel evolutionary development in this genus may have occurred in New Zealand, evidence which suggests a range in age from Neocomian to Albian.

However, samples taken from basalt lava flows in the west bank of the Seymour Stream have yielded the following K-Ar ages (C.J.D.Adams, Institute of Nuclear Sciences, pers.comm. 11.11.88):- (A) lavas outcropping near the junction with the Black Rock Stream, GR S48/739075-7, bottom flow: 96.49 ± 1.36 and 98.12 ± 1.38 Ma, top flow: 94.22 ± 1.40 and 96.43 ± 1.42 Ma; (B) bottom flow of the outcrop of lavas lower down the Seymour Stream, GR S41/725116, 94.07 ± 1.30 and 95.26 ± 1.40 Ma. These determinations indicate a Ngaterian (Late Albian - Early Cenomanian) age for the base of the sequence of volcanics (see *Auldenda*).

1.5. Palaeoclimate

Analysis of palaeomagnetic measurements from both Australia and New Zealand (Schmidt and Embleton, 1981; Oliver, James and Jago, 1983) places south-eastern Gondwana in high polar palaeolatitudes of ca. $70-85^{\circ}\text{S}$ during the Early Cretaceous. Therefore the biotic community would have had to exist under dark seasons of 2 to 4 months duration. As judged from isotopic evidence (Stevens and Clayton 1971), mean sea surface temperature in south-eastern Gondwana was near $14-15^{\circ}\text{C}$ in the late Albian. Axelrod (1984) suggests that even in the dark season the land temperature was probably

never lower than -15°C . The distribution of the continents during the Cretaceous gave broad seaways which were thermally moderating, resulting in low diversity and range of latitudinal climatic zones and, in particular, no ice caps. Thus, at least in coastal regions, the climate was mild temperate and highly equable. The climate of continental interiors could be expected to be somewhat cooler and less equable (cf. Frakes and Francis, 1988). The amount of radiant energy lost during the dark season, and hence the lowest temperature reached, would depend on the amount of volcanic dust and water vapour in the atmosphere.

In recent reviews of Cretaceous palaeoclimate, Axelrod (1984) considered both fossil and modern floras and vertebrate faunas, while Creber and Chaloner (1984) considered fossil and modern wood. Both reviews agree that the Early Cretaceous climate of polar latitudes was able to support plant life without requiring a change in the inclination of the earth's axis, as proposed by Douglas and Williams (1982). Axelrod (1984) pointed out that not only did Cretaceous - Paleogene floras grow within both Arctic and Antarctic Circles, but that today numerous species of trees and shrubs, both conifers and dicotyledons (though more of the latter), range as far north as 73° , ie. well within the Arctic Circle.

Fossil woods of Early Cretaceous age, especially those from Alexander Island west of the Antarctic Peninsula (Jefferson 1982; Francis 1986), then near $65-67^{\circ}\text{S}$, reflect rapid growth rates, high climatic sensitivity and seasonality of growth, features which differ from growth characteristics of modern high latitude trees. Jefferson doubted that the palaeogeographic reconstructions were correct, suggesting that the growth features matched those of living *Phyllocladus* in warm-temperate climate with long growing seasons. However, Creber and Chaloner (1984) showed that the growth features of the Alexander Island trees were consistent with the growth of trees in polar latitudes under mild, highly seasonal (ie. dark) conditions.

1.6. Nomenclature

Mildenhall (1970, p.78) suggests that although Hector's invalid names have been used regularly in New Zealand palaeobotanical literature, "they should not be used further until they have been validly and systematically described." This suggestion is here accepted. A problem also exists in use of

Ettingshausen's generic names, particularly when they are used as a basis for familial associations and palaeobiogeographical analyses (e.g. in Oliver,1950; McQueen,1951). It is here suggested that these generic names not be used or synonymised until the fossils themselves have been reassessed in conjunction with new, more extensive collections where such collection is possible.

It is considered by some palaeobotanists (e.g. Hughes,1976; Krassilov,1977; Crabtree,1987) to be inadvisable to relate Cretaceous fossil angiosperm leaf species to higher taxa other than form genera without clear association with reproductive organs which form the primary basis of angiosperm classification. Even when the reproductive organs are well known, Early and mid Cretaceous plants cannot be unequivocally related to extant taxa at familial or ordinal level (Dilcher and Crane,1984; Nishida,1985; Endress,1986). Indeed the definition of Early Cretaceous "angiospermous" fossils as Angiospermae is considered difficult (Hughes,1984; Mabblerly,1984; Friis, Chaloner and Crane, 1987).

With respect to foliar organs, Friis et al.,(op.cit.) consider angiosperms to be characterised by broad leaves, with vascular bundles forming a reticulate branching pattern with a hierarchical system of successively thinner veins that often have free endings. Furthermore, they consider the dicotyledons to have leaves with the main vein usually pinnate or palmate and the leaf differentiated into a petiole and blade (see also Kaplan,1973; Burger,1981).

It is on this basis that some of the leaves described in this thesis are classified as dicotyledonous. In the absence of corroborative evidence from other organs, no attempt is made to assign species to higher taxa other than form genera. A sole exception is *Liriophyllites parvisinus* sp.nov. The form genera and species described here are based on the leaf architectural features of Hickey(1971,1973) and Dilcher(1974) and the foliar physiognomic types of Upchurch and Wolfe(1987). It is possible that future investigation of cuticular micromorphology may allow the assignment of the leaves to taxa useful in phylogenetic or palaeobiogeographical schemes. New generic and specific names which are phylogenetically nonassociative are coined except where major distinctive characters indicate similarity, but not necessarily relationship, with previously described fossil taxa. The suffix *-ites* is used where a leaf closely resembles a previously described taxon but definite assignment cannot be made (Hickey,1977,p.56). The suffix *-oides* is used where it is not intended that they be permanent names but are proposed as provisional designations (*nomina fluxa*) indicative of resemblance, to be replaced later by correctly formed names (Stearn,1966,p.266).

CHAPTER 2. MATERIALS

As indicated in the historical section of the Introduction, Alexander McKay was the first (in 1885) to make collections of plant fossils from the Clarence valley area. J. Allan Thomson (1913) listed the fossil collections of McKay as coming from Quail Flat at Locality No. GS.560 (61 specimens) and Locality No. GS.568 (174 specimens), and from Red Hill Stream at Locality No. GS.616 (number of specimens not given). The specimens from Quail Flat are housed at the New Zealand Geological Survey, Palaeontological Section, Lower Hutt, under the Locality Nos. B125 and B166 respectively. The whereabouts of the Red Hill Stream specimens is unknown. The number of specimens is impressive since McKay had only a pack-horse for transport. J.A.Thomson made a small collection from the area in 1916 (B146).

D.R.McQueen, collecting in 1953, along with H.E.Fyfe and party, and with similar lack of vehicular support, recovered numerous specimens from several localities in the area. These specimens, including type material, are also in the N.Z.G.S. Collection, under the Locality Nos. B350-361.

The Geological Survey also houses recent collections made by J.I.Raine and Raine & P.J.Oliver (1977), D.Pocknall (1983), and M.B.Reay (1978, 1985) from Horse Flat, middle Clarence valley, totalling approximately 100 collection numbers.

J.D.Lovis and Reay, with the support of various members of the Geology Dept., University of Canterbury, and of the Christchurch office of the Geological Survey, collected specimens totalling 100 numbers during the 1978-79 season. These, together with the collections subsequently made by Lovis and I.L.D., totalling 1022 numbers, are presently housed in the Plant and Microbial Sciences Department, University of Canterbury. On completion of the study, they will be transferred to the Canterbury Museum for permanent curation. Fieldwork for the collection of further specimens was undertaken during the period Nov.1983 to Dec.1987, and occupied a total of 38 days. Fossils in the collections of the Canterbury Museum (Gregg, 1975) and the Otago Museum which constitute the major part of the collections sent to Ettingshausen and Arber have been inspected.

The middle Clarence valley fossiliferous deposits outcrop in ten areas which are relatively isolated from each other (Fig.2.1 and Plates 1-4). Each area is designated as a locality. Within each locality, more than one site may be recognised and may be based on either natural features (e.g.

dissection by a stream) or the number of beds present. For curatorial purposes, the number of beds within a particular site is limited to nine. To date, 33 *in situ* beds and 14 collection sites of loose rock (e.g. river-bed beaches, rock falls) have yielded plant fossils. The number of beds from each locality, with the number of not *in situ* sites in brackets, are:- Red Hill Stream, 1; Horse Flat, 4 (2); Alexander McKay Terrace, 5 (2); East Quail Flat ("southern end" of McKay 1886), 3 (3); West Quail Flat ("upper end" of McKay 1886), 3 (1); Ptilophyllum Ridge, 4; lower Seymour Stream, 5 (2); upper Seymour Stream, 7 (3); Coal Creek, (1); Willows Creek, 1 (see Appendix 4 for Locality, Site and Bed details).

To be able to identify the source of each block of rock collected, beds are numbered consecutively stratigraphically upwards. Where the three-dimensional arrangement of blocks within a bed is known, individual surfaces of blocks are numbered in sequence through or along the bed. When their arrangement is not known, the sequence of "block" numbers is arbitrary. Thus, the Canterbury University (CU) palaeobotany register number CU 456.01 CL represents the lower surface of the first block collected in Locality 4 from Site 5 within Bed 6 in the Clarence (CL) valley. A zero Site and/or Bed number indicates blocks not found *in situ*. Where part and counterpart have been collected, the number is given the suffix a and b respectively. Where a block has been broken during extraction or because of the constraints of transport or storage, the numbers of the separate parts of a particular ^{on adjacent blocks} surface have the suffixes (1), (2), etc. Thus CU 456.01b(3) CL represents the third portion of the counterpart of the surface described above. Where more than one leaf of a particular plant group occurs on a particular surface, the individual leaves are identified by the suffix #1, #2, etc., indicated on transparent overlays to Plates 5-9 of blocks in Volume 2.

This system of numbering was instituted to enable all blocks collected from the same bed to be given the same Bed number, even if collected on different occasions, thus facilitating future ecological and sedimentological analyses. The block number is also used to identify the source of material used for the extraction of cuticle.

Specimens referred to here which are in the N.Z.G.S. Collection have the prefix "B". Under their system, specimens are given a locality number in temporal order of collection, followed by a sequential block number. Specimens in the Canterbury Museum have the prefix "zp", while those in the Otago Museum have the prefix "c".

The fossils occur both as coalified compressions^h and as impressions on eroded surfaces. Schopf (1975) has pointed out that "compression" is the process not the fossil but, in line with common usage, the word is here used to indicate the presence of an albeit thin layer of anthracolemma. Partially ^{permineralized} araucariacean wood samples have been collected from Willows Formation at West Quail Flat, but no other petrified material has yet been obtained.

Phyllopteroides pinnules occur in both mudstone and sandstone, in six beds from only three localities. They are very fragile, and have been excavated only with difficulty.

Taeniopterid fossils occur at six localities in at least 21 beds. The majority are incomplete leaves; of 76 leaves measured, 6 adult and 5 juvenile leaves are almost or actually complete. Many more fragments are clearly taeniopterid but were unmeasurable for the characters considered (see Section 5.3).

Although compression fossils of cycadophytes have been obtained from all localities except the lower Seymour Stream and the Willows Stream areas, each species is relatively restricted in occurrence. Furthermore, only *Ptilophyllum seymouricum* and *Pterophyllum rectipinnatum* are even locally abundant. The former is abundant in cross-bedded sandstone at Ptilophyllum Ridge, but is sparse in crevasse splays at Alexander McKay Terrace and East Quail Flat. The latter is fairly abundant both in crevasse splays and "local" mudstones at Horse Flat, and in mudstones, sandstones and tuffs in the upper Seymour Stream area. This pattern of occurrence suggests the cycadophytes ^{may have} formed part of the understory of local forests.

As part of the taxonomic investigations of taeniopterids and cycadophytes, specimens on some 80 blocks in the N.Z.G.S. Collection and the National Museum from other New Zealand Mesozoic sites were inspected.

Ginkgo occurs as compression fossils in most localities within the study area. However, while they are very common in certain mudstone beds at East Quail Flat, they are sparse in mudstones in other localities, and rare in sandstone beds everywhere. In mudstone samples, the fossil may be lifted whole from the rock surface after drying, and may be used for preparing cuticle by standard maceration techniques.

Araucariacean leaf fossils occur as compression fossils in all localities within the study area. In mudstone samples the fossil may be lifted whole from the rock surface after drying. In sandstone

samples, differential fracture yields rock fragments which may be used for preparing cuticle by standard maceration techniques.

For the comparison of fossil *Agathis* cuticle with that of extant species, herbarium samples of twelve extant *Agathis* and two *Araucaria* sect. *Columbea* specimens were macerated using the same procedure as for preparation of the fossils. The taxa investigated, their source and, where applicable, their synonymy in Whitmore's 1980 revision are presented in Table 8.1 and Appendix 3.3. The names cited are those to which the respective collections are attributed in the CANU and CHR herbaria, and are retained for presenting results.

Dicotyledonous leaf fossils occur in 32 beds in eight of the nine localities within the study area. The remaining 15 beds sampled lacked dicotyledonous leaves. More than 882 leaves ^{in the collection} were inspected. Of these, 656 are assigned to one of 22 new form species. The quality of a further 136 is such that with further study it may be possible to assign them to present or new form species. More than 90 leaf fragments are unable to be assigned and are not likely to be in the future (Table 9.1, Appendix 5).

CHAPTER 3. METHODS

3.1 Excavation of Fossils

The fossils occur both as coalified compressions (see Chapter 2), and as impressions on eroded surfaces. Field techniques for the exposure of coalified fossil material *in situ* varied according to the type of rock being excavated. In finely laminated mudstone, fossil leaves are usually lying on the bedding planes, and careful splitting with a thin blade produced well exposed fossils. In bedded sandstone, impact with a hammer split the rock along a bedding plane exposing any fossils in that plane. Numerous fossils in a particular plane increases the probability of fracture in that plane. However, in massive sandstone such as occurs in a crevasse splay, impact usually results in irregular fracture which may or may not expose all of a particular fossil leaf.

Where fracture failed to expose all of a leaf, hidden parts were exposed in the laboratory by a technique similar to *dégagement*, or by "differential fracture". The former is a well-known technique employing gentle impact of a fine needle to remove overlying rock particles grain by grain. If carefully applied, this technique leaves the whole fossil intact, but no material suitable for cuticle analysis is produced. In this study, a fine needle was used for removal of small fragments and/or particles of rock overlying fossils in mudstone or uncemented sandstone. In the case of fossils in cemented sandstone, the nature of the rock and the thickness of carbonaceous material usually resulted in bent needles or deep punctures of the fossil. Attempts to use a vibratool for exposure of these fossils were unsatisfactory. Therefore the technique here termed differential fracture was employed.

Differential fracture takes advantage of the difference in strength between the coalified fossil and the enclosing rock. A chiselled or pointed punch is held in a suitable position relative to the fossil and hit with a light hammer. Usually several blows are required. When impact is sufficient, fracture through the rock between punch and fossil produces a chip of rock bearing the uppermost layer (including cuticle) of the fossil. This fragment may be used as a cuticle sample or may be glued to the counterpart. The type of punch used, and its position relative to the fossil depend upon the thickness of overlying rock and the part of the fossil being excavated. When the overlying rock is thick, or when working beyond the margin of the leaf, the chisel punch is preferred. It tends to produce "large" (up to 1

cm²) fragments. When the overlying rock is thin (especially when forming a layer between two adjacent fossils) or when working to clear the margin or petiole of a leaf, the pointed punch is preferred as excessive damage is less likely. In the former "sandwich" situation, "very large" (up to 5 cm²) fragments may be produced. In the latter, "small" (5-10 mm²) fragments are produced.

Transfer of fragments from part to counterpart produces extra information by (perhaps) completing both adaxial and abaxial surfaces of the leaf so that both may be used for measurement of characters. The rock surfaces of fragments were wetted, the fragments positioned on the block, and then fixed by applying water-soluble P.V.A. droplets with a needle to the edges of fragments. By ensuring water did not flow on to the fossil itself, glue dispersing along the fine films of water between block and fragments did not obscure the fossil. Similar glueing procedure was used to "reassemble" blocks fractured during field excavation, especially when the fracture crossed a valuable fossil.

3.2. Cuticle Preparation

Samples for cuticle preparation of fossils occurring in mudstone were obtained by bulk maceration with HF, or (for *Ginkgo* and *Agathis* fossils) lifted whole from the rock surface after drying. In sandstone samples, differential fracture yields rock/fossil fragments bearing the adaxial or abaxial cuticle of the leaf depending on whether the part or counterpart is excavated.

Standard maceration procedure (Harris 1956, Stace 1965) was tried initially for all plant types. Rock fragments were immersed in HF for a period sufficient to digest all rock leaving free carbonaceous material. This was digested in Schultze's mixture (5 mg KClO₃ per ml conc HNO₃) for 6 to 24 hours until only the cuticle remained ^{(see Addenda).} Some samples required mechanical separation and removal of "mesophyll", followed by further digestion in 1% CrO₃ and/or Schultze's mixture. Samples of both adaxial and abaxial cuticle were washed in water and mounted in glycerine jelly containing safranin stain on glass slides for light microscopy. Similar washed samples were mounted on S.E.M. stubs with double-sided cellotape and air dried. After sputter-coating with gold (50 n.m.) they were photographed with a Cambridge Stereoscan 250 MkII S.E.M., using either secondary electrons (S on S.E.M. micrographs) or backscatter electrons collected by a Robinson detector (C on S.E.M. micrographs).

Cuticular micromorphology is essential to determine the order to which a taeniopterid taxon belongs. A similar situation obtains for the pinnate cycadophytes. Attempts to isolate cuticle from taeniopterid samples by standard maceration procedures failed apart from tiny fragments from *Nilssoniopteris* sp. Limited success was achieved for *Nilssonia elegans* by the *in situ* method (see below). No cuticle was obtained from *Taeniopteris stipulata* samples.

In the case of pinnate cycadophytes, cuticle extraction by bulk maceration of rock/fossil fragments obtained by differential fracture was satisfactory only for *Pterophyllum rectipinnatum* (Plate 15D-F) and *Ptilophyllum seymouricum* (Plates 18-19). It was difficult to prepare cuticle of the latter which was clean and with anticlinal flanges still intact. Furthermore, if digestion was continued long enough to remove all carbonaceous material, only the thickened portions of the guard and subsidiary cells retained detail (Plate 19E,F). The cuticles of other species proved to be too fragile to maintain its integrity during maceration. Substitution of Schultze's mixture with H_2O_2 only slightly improved the situation. However, when the rock/fossil fragments obtained by differential fracture were treated with 40 vol H_2O_2 for two to three days, most of the carbonaceous material, except for veins, was digested, leaving fragments of cuticle with the internal surface uppermost, adhering to and supported by the rock surface. The rock fragment was mounted on a SEM stub using "copper print", then coated and photographed in the usual manner (e.g. Plates 15A, 16H). This *in situ* cuticle, though fragmentary, is displayed in burial position, and therefore, when photographed with the S.E.M., may be used to measure the arrangement and dimensions of cells with confidence.

Preparation of cuticle from herbarium specimens of araucariacean leaves followed standard procedures. A sample approximately 1 cm^2 was cut from the medial area of a leaf so as to include the margin, digested in Schultze's mixture for 6 to 24 hours until the cuticle could be peeled, then soaked in conc HNO_3 saturated with CrO_3 (or 10% CrO_3 if delicate) until the mesophyll, hypodermis and epidermis were digested. Some samples required mechanical separation and removal of mesophyll followed by further digestion in 1% CrO_3 and/or Schultze's mixture. Subsamples of both adaxial and abaxial cuticle were mounted and photographed in the same manner as the fossil cuticle.

Attempts to extract dicotyledonous cuticle by the standard method resulted in small fragments of cuticle, some of which appeared to have been punctured by sand grains. Apparently the cuticle is too thin or too fragile to remain coherent. Attempts to produce useable cuticle by the *in situ* method have so

far been unsuccessful. Refinement of the *in situ* method using weaker oxidising agents and longer digestion times may prove successful.

3.3. NUMERICAL TAXONOMIC ANALYSIS

3.3.1.a Cluster Analysis:

Cluster analysis uses association coefficients as measures of similarity and hierarchically clusters Operational Taxonomic Units (OTUs) (here representing individual leaves) on overall resemblance. Association coefficients of the OTUs for the characters selected are calculated using Gower's coefficient (Gower, 1971). The resultant matrix is subjected to cluster analysis using unweighted arithmetic average linkage using the MINT6 programme (Rohlf, 1971). The resultant empirical clustering is presented as a phenogram. The phenogram is used subjectively to form groups of OTUs with minimum "within group" variation and maximum "between group" variation. This serves to confirm *a priori* groups (e.g. form species) and to identify misclassified OTUs. Data for cluster analyses are given in Appendix 3.

3.3.1.b Discriminant Analysis:

Stepwise discriminant analysis was carried out using the BMDP7M computer programme (Dixon 1981) (see also West and Noble, 1984). The programme selects at each step the character which best discriminates between *a priori* groups and enters it into the discriminant function. The criterion for entry is "F-to-enter" which is the F statistic computed from a one-way analysis of covariance, where the covariates are the previously selected characters. The numerical value of F-to-enter is set to a predetermined value, either 2.0 or 4.0. Thus the particular characters statistically significant in discriminating between *a priori* groups and their relative importance are determined.

Where the cumulative proportion of total dispersion for the first two canonical axes is high, most of the variability is being expressed in a few dimensions. This may imply correlated discriminating abilities among the characters, hence low F values. Those characters with very low F values would not

normally be entered into the classification function. To gain some idea of the order of relative importance of characters not entered into the function, their non-entry is overcome using the program option Force = 1 (Dixon 1981, p.533). This option "forces" the characters into the classification function without regard to the F-to-enter limit and retains them in the classification regardless of the influence of other characters.

Dixon (1981,p.534) states "Mahalanobis D square and the posterior probabilities are computed for each [OTU] after the final step of the discriminant analysis. The Mahalanobis D square used is the distance from each [OTU] to each group mean. Both the group mean and the cross-products matrices use the [OTU] in the computation of the cross products". Groups with only one OTU must have zero within-group variance for all characters and are therefore represented in character-defined hyperspace only as a point. This difficulty is overcome by using the "jackknife" option. "When "jackknife" is specified in the discriminant function, each [OTU] is eliminated in turn from the computation of the group means and cross products; D and the posterior probability are computed for the distance from the [OTU] to the groups formed by the remaining [OTUs]" (Lachenbruch and Mickey, 1968)" (Dixon 1981, p.534).

The programme also tests each OTU against the mean established for its group and, where significant difference exists, indicates the group with which any incorrectly classified specimens are truly most closely associated.

The BMDP7M program produces coordinates of the first two canonical variates for a scatter plot. Since a scatter plot cannot be directly compared with a phenogram, a programme specially written by Chris Frampton was used which makes use of these coordinates of the first two canonical variates to calculate the euclidian distance between OTUs which is equivalent to the Mahalanobis D square values in two dimensional discriminant space. These euclidian distances were then used as a similarity matrix to produce a phenogram of the grouping, again using the MINT6 programme (cf. Figs. 8.2.a and Fig. 8.3).

3.3.1.c Numerotype:

Variation of dimensions or states of characters exists between individuals assigned to a particular taxon. The problems of handling such variation has been addressed by Hughes (1976) who has proposed a "Code" for palaeontological data. However, to compare taxa within a set of similar taxa

numerically, it is desirable to select an individual which fairly represents the variation within each taxon, thereby avoiding unnecessarily large data bases created by inclusion of all individuals. Furthermore, under present taxonomic constraints, an individual specimen must be designated as the holotype for formal diagnosis of the taxon.

For a taxon distinguished from others in a set by one or two characters which show no variation within the taxon, selection of a suitable individual is simple. For a taxon distinguished by a number of characters, one or more of which show variation within the taxon, selection of a representative individual is difficult. To overcome this difficulty, parametric analyses of continuous characters, together with discriminant analysis to identify the characters which best discriminate between taxa in a set, is used to establish which individual best represents the taxon. This individual is here designated the numerotype for that taxon. The dimensions and states of characters of the numerotype are used for numerical comparison with other taxa. As a consequence, variation within a taxon is disregarded in such analyses. For formal description of the taxon, the numerotype is designated as the holotype and used as the basis for the diagnosis. Nevertheless, variation within the taxon is accommodated within the description. For further discussion of methods involved in numerotype selection, see Sections 3.3.2.c, 9.4.1.a(i) and 9.4.1.c(i).

3.3.2.a. Taeniopterid Leaf Characters

Of the 76 taeniopterid leaves measured only six adult and five juvenile leaves are almost or actually complete. They were measured for the following characters:- maximum lamina width, maximum midrib width, and angle of secondary veins to the midrib. The last comprises two measurements i.e. vein angle on each side of the midrib. Where variation occurred along the leaf, the "most common" angle was used. However, since angles were measured "within 5⁰ increments" this was, in practice, not a great problem. Individual fossils were allocated to one of three taxa (*Taeniopteris stipulata*, *Nilssonia elegans* or *Nilssoniopteris* sp.) according to the presence of the characters listed in Table 5.1. Where crucial character combinations were lacking, allocation was by "best guess"; this lack of characters is particularly

common for basal-medial fragments. Also, a particular character may show some variation within a taxon.

A fourth taxon referred to here as a "linearphyll", while straplike with a prominent midrib, apparently lacks secondary veins. Thirteen such linearphyll leaves were measured for lamina and midrib widths and are included in the analysis for comparison with the values for *T.daintreei* of Blaschke & Grant-Mackie (1976).

The data were subjected to stepwise discriminant analysis. Where misclassifications were indicated, the individuals were reassessed as to their taxonomic placement and where considered reasonable, individuals were reallocated to the appropriate group and the programme rerun. By this process of refinement, and excluding juveniles and linearphylls, the number of taeniopterids used in the discriminant analysis was reduced to 64.

Stepwise discriminant analysis, firstly of all four taxa, secondly of only the first three, was used to establish which character(s) distinguished the taxa. Comparison of mean lamina widths of taxa using t-tests were carried out to establish the probabilities of taxa belonging to the same statistical population.

3.3.2.b. *Agathis* Cuticular Micromorphological Characters

A preliminary study of *Agathis australis* ^{using t-tests} showed statistically significant differences in dimensions of cells in apical, medial and basal regions of the leaf and between corresponding areas of adaxial and abaxial surfaces. Therefore all samples were taken from the medial region of a mature leaf so as to include the margin (see also Stace 1965 p.22).

Comparison of the cuticular micromorphology of *A.seymouricum* with that of 14 extant taxa (Table 8.1) was carried out by cluster analysis of association coefficients for 35 characters (Table 8.2) and by stepwise discriminant analysis. The characters employed were chosen on the basis of the possibility of measuring them in the fossil and mostly follow those of Dilcher (1974). Measurements were made directly from the S.E.M. photographs.

To allow comparison of the clustering derived from cluster analysis with the taxonomic treatment of Whitmore (1980) and the leaf groups of Page (1980), stepwise discriminant analysis was

carried out to produce Mahalanobis D square values for each OTU relative to the means of *a priori* groups.

The detailed composition of the *a priori* groups varies according to circumstance, and was determined according to the taxonomic scheme being tested. The groups are given informal names for discussion purposes (Table 8.3). Thus the "robusta" *a priori* group included OTUs 4, 11, 12 for testing Whitmore's scheme, but included OTUs 4, 5, 7, 11, 12 for testing Page's 'A' scheme. Groups may also be selected to test the ability of the character set to reflect, for example, geographic distribution or ecological variation.

Cluster analysis was used to assess similarities between *A. australis*, *A. seymouricum*, *A. clarencianum* and the Australian fossils *A. yalloumensis* and *A. parwanensis*.

3.3.2.c. Dicotyledonous Leaf Characters

Each leaf (previously assigned a unique identifying number, see Chapter 2) was assessed for the major characters of leaf architecture described by Hickey (1971, 1973) and Dilcher (1974) together with those established during the study (see Section 9.2). Where present, both part and counterpart were used for measurement of characters.

If a leaf corresponded in major characters, particularly secondary vein pattern, to a previously assessed leaf, it was assigned to a tentative "leaf form" which included all similar leaves. If it differed by more than a few characters a new "leaf form" was established. When all the leaves in the collection (up to Dec. 1987) had been assessed, all the leaves assigned to each "leaf form" were compared with each other to ensure the "within group" variation was not too great, since the tendency had been to "lump" rather than "split". While all the characters of Dilcher (1974) were measured, it became apparent that certain ones were of more value than others in establishing the "between group" variation. Where a "leaf form" was judged to be sufficiently taxonomically distinct it was elevated to the status of a form species. Twelve of the form species established so far had a single character or a combination of two or three characters which clearly differentiated them from other forms. However a further nine form species were established on a combination of four or more characters. Most of these potentially diagnostic characters showed variation within a form species.

To establish firmly these nine multi-character form species, 102 leaves were measured for 16 characters which distinguished one or more form species (Section 9.4.1). These data were subjected to simple parametric analyses, cluster analysis and discriminant analysis.

Standard deviations of the continuous characters served to establish the amount of "within group" variation. Group means of the continuous characters allowed the identification of the leaf potentially the most suitable as the numerotype for each form species (see Section 9.4.1.a.i). Correlation coefficients, skewness and kurtosis of all characters identified the characters most suitable for cluster analysis (see Section 9.4.1.a.ii).

The phenogram resulting from cluster analysis was used subjectively to form groups of OTUs with minimum "within group" variation and maximum "between group" variation. This served to confirm 10 *a priori* groups (form species; see Section 9.4.1.c.i) and to identify misclassified OTUs.

Discriminant analysis indicated the relative discriminatory value of the characters in forming these form species. It was also used to confirm that the specimen selected as the numerotype for each form species using the means of continuous characters was the most suitable specimen in terms of the discriminant characters.

Measurements of 30 characters which distinguish between two or more form species were made on the numerotype selected for each of the 22 form species (i.e. 22 OTUs). These data were also subjected to cluster analysis. This served to establish five groups of form species based on overall resemblance. Discriminant analysis of these data identified the characters effecting this grouping, but gave no indication of the "biological reasoning" behind such grouping. Similarly, analysis of the standardised coefficients for canonical variables failed to establish clearly the basis of the grouping. The systematic survey of dicotyledon leaf architectural features outlined by Hickey and Wolfe(1975) is not able to be used because not all of their characters are available in the fossils due to the state of preservation or absence of certain characters. However, use of the characters suggested by Upchurch and Wolfe(1987,p.76) permits good correlation of four of the five groups with their "foliar physiognomic types"(loc.cit.,p.82) and therefore are used as the basis for describing the six form genera here proposed. On-line search of "Biosis Previews 69-88" and "Georef - 1785-1988" was used to establish originality of the generic names.

4.1. Introduction

The form genus *Phyllopteroides* was erected by Medwell (1954) for some distinctive Australian leaf species formerly referred to *Phyllopteris* Brongniart 1849 or *Linguifolium* Arber 1913. Cantrill and Webb (1987) reappraised the genus in the Early Cretaceous of eastern Australia, and suggested it is an osmundaceous fern. They allocated the leaves to four species (including two new species), three of which occur in successive stratigraphic horizons in the Victorian Early Cretaceous and suggested a probable evolutionary lineage. Furthermore, they revised the Early Cretaceous megafloal zonation of Douglas (1969) by defining the zone boundaries as the first occurrence of the *Phyllopteroides* species nominated for each zone.

McQueen (1956) described pinnae (loc.cit.p.682, Text-Fig.2, Figs.10-12) from Quail Flat (B125/34, B125/61) and the Paparoa Coal Measures (B19/39, B19/40) and referred them to *Phyllopteris expansa* Walkom. However, Cantrill & Webb (1987, p.63) doubt the generic assignment of Walkom's specimens and suggest this species should be referred to *Sphenopteris* Brongniart. McQueen also described an oblong pinna (loc. cit.p.682, Text-Fig.2, Fig.13) from the Paparoa Coal Measures (B23/1 & B172/5) and referred it to *Phyllopteris lanceolata* Walkom. It may be correctly¹⁰ referred if McQueen is in error in describing the midrib as not persisting to the apex (cf. Cantrill & Webb, 1987 p.68 "persisting to just below the apex"). Re-examination of McQueen's specimens is required to assess their true relationships, both generic and specific.

Fossils described below from the middle Clarence valley are divided into four informal groups based on location and pinnule form (Table 4.1, Plate 11). Data for individual pinnules are presented in Appendix 3.1. These groups do not correspond sufficiently well with the species described by Cantrill & Webb (1987) to allow assignment to those taxa. However, it is felt that insufficient data are presently available to allow their description as separate species. They do show characters sufficiently similar to the Australian species to indicate similar evolutionary trends.

4.2. Description of Pinnule Groups (Figures 4.1 - 4.4)

Group 1 consists of 13 pinnules from Alexander McKay Terrace (Table 4.1) which are generally elliptic, 20+mm. to 50+mm. long and 11 mm. to 25+mm. wide, with serrate margins in the apical portion, teeth generally smaller than 1 mm. at a density of 10 - 24 per 10 mm. of margin and secondary vein density of 12 - 26 per 10 mm. of margin. These characters correspond well to those of *Phyllopteroides laevis* Cantrill & Webb. However several specimens (e.g. 220.09(1)#1, Plate 11A) are clearly biserrate in middle and basal portions of the margin, have 1 and 2 veins per tooth and have a secondary vein angle of 51° to 73° . Biserrate teeth do not occur in any of the species of Cantrill & Webb. The presence of 2 veins per tooth excludes these pinnules from *P.laevis*. The high angle of secondary veins accords only with *Phyllopteroides lanceolata* (Walkom) Medwell, but the overall shape, margin, high dentation density and low vein density excludes them from that taxon. They may represent a form intermediate between *P.laevis* and *P.serrata*.

Group 2 consists of 6 pinnules from the upper Seymour Stream (Plate 11B) which are generally ovate, 15+mm. to 42+mm. long and 10 mm. to 20+mm. wide with serrate margins, teeth smaller than 1 mm. with 1 and/or 2 veins per tooth and a vein density of 12 - 18 per 10mm. of margin. These characters correspond well to those of *Phyllopteroides serrata* Cantrill & Webb. However, they have a dentation density of 8 - 15 per 10 mm. of margin and secondary vein angle of 47° to 76° , both of which are well above the corresponding ranges for *P.serrata* (Fig.4.3).

Group 3 consists of five pinnules from West Quail Flat which are generally linear-lanceolate, 15+mm. to 40+mm. long and 10 mm. to 20 mm. wide, with entire and/or dentate margins. Only one specimen (412.47, Plate 11C) has a significant amount of its margin dentate. It has teeth 2.5 mm. long with 2 to 4 veins per tooth, and a dentation density of 6 per 10 mm. of margin. The group has a vein density of 12-18 per 10 mm. of margin and secondary vein angle of 35° to 45° . One specimen (412.45a, Plate 11D) has a long tapering base as in Cantrill & Webb (1987) Fig.7E, but the others (e.g. 411.20#2, Plate 11E) have acute cuneate bases as in (loc.cit) Fig.7A. When five partial specimens with acute cuneate bases are included, the secondary vein angle range is widened to 27° to 49° . These characters correspond well to those of *Phyllopteroides dentata* Medwell except that the dentation density, vein

density and secondary vein angle *almost* reach the lower values of the range for these characters in (cf. Figs. 4.1 and 4.2) *P.lanceolata*. The small pinnule size does not correspond with "normal" *P.dentata* pinnules, but is similar to a small number of pinnules from Victorian sediments not included in Cantrill and Webb's analysis (pers. comm. D.Cantrill, Aug. 1988).

Group 4 consists of one pinnule (411.20#1, Plate 11F) from West Quail Flat which is wide elliptic (see Fig.9.2), 15+mm. long and 10 mm. wide, with a dentate margin with teeth 0.2 mm. long and 2 to 3 veins per tooth, dentation density of 11 per 10 mm. of margin, vein density of 30 per 10 mm. of margin and secondary vein angle of 64° . These characters correspond well to those of *Phyllopteroides lanceolata* (Walkom) Medwell except for the pinnule shape which is oval-lanceolate to lanceolate in *P.lanceolata* (Cantrill and Webb 1987,p.68).

4.3. Application to Clarence Groups of Characters used to distinguish Australian Species

Cantrill & Webb (1987, p.64) list six characters by which *P.laevis* may be separated from *P.serrata* and *P.lanceolata*. When these criteria are applied to the corresponding Clarence groups (Groups 1, 2 and 4 respectively), the assignments indicated above conform well except for the fifth and sixth characters. Thus:

1. Group 1 pinnules are generally longer than those in Groups 2 and 4.
2. Group 1 pinnules have fewer veins per tooth than Groups 2 and 4.
3. Group 1 vein density range encompasses those of Groups 2 and 4.
4. Groups 1 and 2 pinnules have attenuate bases and the Group 4 pinnule base is shortly attenuate.

5. Cantrill and Webb (loc.cit.) state that *P.laevis* is more elliptical than either *P.serrata* (ovate to lanceolate) or *P.lanceolata* (oval-lanceolate to lanceolate). Group 1 pinnules are indeed more elliptical than Group 2 pinnules (ovate) but are generally more narrowly elliptical than the Group 4 pinnule which is wide elliptic.

6. Groups 1 and 2 pinnules have secondary vein angle ranges ($51-73^{\circ}$ and $47-76^{\circ}$ respectively) which are more characteristic of *P.lanceolata* ($50-70^{\circ}$) than *P.laevis* or *P.serrata* ($45-60^{\circ}$). The Group 4 pinnule secondary vein angle (64°) is within the range of *P.lanceolata*.

Cantrill and Webb (1987, p.73) plotted venation angle against pinnule width to distinguish between *P.dentata* and *P.lanceolata*. When the Clarence pinnules of Groups 3 and 4 are superimposed on their plot (Fig.4.1) the pinnule of Group 4 (A) falls within the range of *P.lanceolata*, while the pinnules of Group 3 (B-K) ^{collectively and surrounded} fall within the range of *P.dentata*.

Cantrill and Webb (loc.cit.) also plotted pinnule shape (expressed by the ratio of distance from base to the point of maximum width divided by the total pinnule length) against pinnule width to distinguish between *P.laevis*, *P.serrata* and *P.dentata*. The Clarence pinnules are rarely complete. An estimate of pinnule shape may however be gained by using the actual length of pinnule preserved to obtain a maximum value of the ratio. Specimens thus estimated are indicated in Fig.4.2 by a downward arrow. Superposition of the Clarence pinnules on the Cantrill and Webb plot (Fig.4.2) shows that Group 1 pinnules (1-8) show general agreement with *P.laevis*. In Group 2 (9-12), three of the four pinnules have (estimated) low values as expected for *P.serrata*. Only two of the Group 3 pinnules (13, 14) were usefully able to be estimated. Both fall within the range for *P.dentata*.

The character showing the least correlation with those of Cantrill and Webb (1987) was secondary venation angle. Cantrill and Webb (pers.comm. D.Cantrill, August 1988) measured the secondary vein angle of a particular vein as the angle between the midrib and the segment of vein which maintained constant direction across the lamina. The secondary vein angle recorded for a particular pinnule is the mean of five such measurements of veins in the midsection of the pinnule. Thus ranges given by them (Cantrill & Webb, 1987) are for variation between pinnules. Measurements in the present study were made prior to knowing the exact criteria used by Cantrill & Webb.

In the Clarence pinnules, vein angle was found to vary consistently along the pinnule, being wider basally and narrower apically. Thus, a mean value obtained from a number of measurements along a pinnule would have depended on the random choice of veins rather than on any intrinsic difference between pinnules. It was therefore considered that the vein angle most useful for comparison of pinnules was the widest angle achieved by a secondary vein reaching the margin beyond the "base" (i.e. where dentation had begun), regardless of position along the pinnule.

4.4. Cluster Analysis

Cluster analysis (see Section 3.3.1.a) of 25 OTUs for the eight characters margin, width, form, veins per tooth, maximum tooth size, tooth density, vein density and vein angle (see Appendix 3.1 for character states and data), maintains the four groups as detailed above (Fig.4.4). The group 4 specimen (OTU 22) is loosely clustered with Group 1 specimens because of its shape (elliptic) and high vein density, but is separated from them because of its margin (dentate) and number of veins per tooth (2 to 4). One of the Group 3 specimens (OTU 25) is partially separated from the others because it is the only one with a dentate margin and hence data on veins per tooth, tooth size and tooth density. It also differs in shape (elliptic). Group 3 is more distinctly separated from the other groups than they are from each other because of margin, pinnule shape and low secondary vein angle.

4.5. Evolutionary Trends

The stratigraphic order for the Clarence pinnules, in upward succession, is Group 1 (Alexander McKay Terrace, probably some considerable thickness below the volcanics), Group 2 (upper Seymour Stream, immediately below the volcanics dated 98 Ma.) and Group 3 and 4 (West Quail Flat, above the volcanics dated 95 Ma.). These groups show trends similar to the evolutionary trends indicated by Cantrill and Webb (1987,p.78) for Australian *Phyllopteroides* spp. Thus the oldest form (Group 1) is finely serrate with 1 or 2 veins per tooth while the youngest (Groups 3 and 4) are strongly serrate (or entire) with 2 to 4 veins per tooth. Group 2 pinnules have an intermediate morphology. Accompanying the increase in the development of the dentation are increases in the size of the teeth and the spacing between them, and decreases in the vein density (Fig.4.3). The pinnule shape shows a similar trend to the Australian species from elliptic (Group 1) to ovate (Group 2) to lanceolate (Groups 2 and 3) to oblanceolate (Group 3) accompanied by a decrease in the venation angle. The single specimen in Group 4 here occurs with Group 3 (cf. *P.lanceolata* in Queensland and *P.dentata* in Victoria) but fits into most of the trends described above. Thus it is wide elliptic in shape and has margins with well developed

dentation and several veins per tooth. However it maintains the high venation density and wide venation angle of earlier forms.

5.1. Introduction

The fossil leaves from the study area which could be attributed to the form genus *Taeniopteris* Brongniart (Plate 12) are assigned to one of three form species. Each is a simple, strap-like leaf with a prominent midrib and numerous, often bifurcating, secondary veins running out to the margin at between 65° and 90° to the midrib. The overall leaf shape, apex, base and margins of more or less complete leaves serve to distinguish them from each other but, when only the middle section of the leaf is preserved, separation is difficult.

A review of previously described New Zealand Mesozoic taeniopterids, and a revision of the Jurassic taxa are presented in Appendix 2.1. Comparison of the present fossils with these revised taxa using gross morphological features allows attribution of most of the Clarence fossils to either *Taeniopteris stipulata* Hector ex McQueen 1956, or *Nilssonia elegans* Arber 1917. The remainder are attributed to a new form species here described as *Nilssoniopteris* sp. A fourth taxon, *Taeniopteris arctica*, here equated with the pteridophyte *Taeniopteris batleyensis* Edwards 1926, is very rare in the middle Clarence valley. It is discussed (Section 5.2) but not described.

Consideration of their cuticular micromorphology and/or their gross morphological affinities suggests the three taxa described belong to three separate orders of gymnosperms, viz. Pentoxylales, Cycadales and Bennettitales respectively.

5.2. Taxa Previously Described from the Cretaceous of New Zealand

Confusion surrounds both the identity and the age of taeniopterid leaves attributed by Hector to *Taeniopteris obtusatus* and *T. stipulata*. It should be noted that the former name was never validly published; the latter was later validated by McQueen (1956) as described below. In 1870 (Hector, 1870, p.199), he listed "*T. obtusatus*" from Mataura Falls (Jurassic) and "*Taeniopteris*" from Pakawau

(Cretaceous). In 1880 (Hector, 1880, p.48) he listed "*Oleandridum obtusatum*" and "*O.stipulatum*", both from the Jurassic. In 1886 (Hector, 1886a, p.31), he listed "*T.obtusatus*" from Mataura, Clent Hills and Waikato Heads and "*T.stipulata*" from Waikawa (all Jurassic), and (op. cit. p. 32), "*T.obtusatus*" from Pakawau and Quail Flat, Clarence. Later (Hector, 1886b, p.61, Fig.24A.3), he figured an inaccurate sketch and labelled it "*Taeniopteris stipulata* (Pakawau)". A specimen from Clent Hills in the NZGS collection, B63.5 (counterpart B69.1) was figured in Hector's "unpublished plates" (PL.II, Fig.16). The same specimen was figured by Arber (1917, PL.VIII, Fig.7) and named *Taeniopteris thomsoniana*. It is accompanied by a card in an unknown hand labelling it "*T.obtusatus*". These facts suggest that the name *T.obtusatus* should now be treated as a synonym of *T.thomsoniana* Arber.

Park (1887) as well as Hector applied the name *T.stipulata* to leaves from Waikawa. The only taeniopterids described by Arber (1917) from Waikawa were assigned by him to *Taeniopteris vittata* Brongniart. This suggests that *T.stipulata* of Park and Hector from Waikawa should now be treated as a synonym of *T.vittata* sensu Arber (but see Appendix, 2.1). Indeed NZGS specimen B77.22 from Waikawa, which is illustrated in Hector's "unpublished plates" PL.XIII, Fig.17, is labelled "*Taeniopteris stipulata*". From the same collection and location, specimen B60.8 is illustrated both in Hector's "unpublished plates" PL.XIV Fig.22a and in Arber (1917) PL.VI, Fig.2 (the latter named as *T.vittata*).

Thus while Hector applied *T.obtusatus* to both Jurassic and Cretaceous leaves, he applied *T.stipulata* only to Jurassic leaves apart from one exception. This was the named sketch in Hector, 1886b.

Of several leaves illustrated in Hector's "unpublished plates" PL.XXVII and XXVIII, which were said to originate from Pakawau, one (PL.XXVIII Fig.37, NZGS specimen B161.24) was identified by McQueen (1956) as the one inaccurately figured by Hector 1886b (ref. above) as "*Taeniopteris stipulata* (Pakawau)". He selected it as the lectotype for *T.stipulata* Hector (McQueen 1956, p.683 Text-Fig.3, Fig.4). He also illustrated a leaf from Shag Point (loc. cit. Text-Fig.3, Fig.5, Hector "unpublished plates" PL.XXVIII, Fig.40, NZGS specimen B160.105) and one from Quail Flat (loc. cit. Text-Fig.3, Fig.7, NZGS specimen B358.8). By his choice of samples, McQueen appears to restrict the application of *T.stipulata* to fossils of Cretaceous age.

McKay (1886) referred to the frequent occurrence of "*Taeniopteris*" leaves in the middle Clarence valley and at Shag Point but does not give them a specific identity.

Edwards (1926, p.124) described a fern with circular sori close to the midrib from the Cretaceous rocks at Kaipara Harbour as *Taeniopteris batleyensis*. It has secondary veins at right angles to the midrib which fork close to the midrib or beyond the sori. Those forks close to the midrib have a distinctive U shape (pers. obs.). The vein density beyond the forking is approximately 15/cm. (cf. 15-30/cm. for *T.daintreei*, 18-50/cm. for *T.stipulata*, 24/cm. for *Nilssoniopteris* sp., and 40/cm. for *Nilssonia elegans*). Edwards pointed out (loc.cit) that "the reference of the fertile frond to the form-genus *Taeniopteris* is purely provisional".

Arber (1917, p.44) described leaves which "in some respects very closely resembles *T.daintreei* McCoy in habit ... [but] ... differs, however, in the nervation, the nerves being conspicuous and comparatively distant". These leaves also have a distinctive U-shaped forking of lateral nerves (pers.obs.). Arber placed them in *T.arctica* Heer, and (loc.cit.) quoted Heer's diagnosis for the fronds "from the Cretaceous of Greenland" which includes in part "*soris rotundatis, biseriatis, nervo medio approximatis*". It is thus clear that Arber believed that these New Zealand leaves belonged to a fern.

He gives the locality from which these fossils had been obtained as "Waikato Heads (Neocomian)" and states (loc. cit.) "Fragments of this frond also occur on the large specimen figured in Plate XIV, but are not seen in the photograph". This "large specimen" (B161/30) also bears dicotyledonous leaves and was shown by McQueen (1955) to have come from Cretaceous strata at Pakawau. Of the leaves illustrated by Arber as belonging to *T.arctica* only that figured in PL.VI, Fig.1 remains in the New Zealand Geological Survey collection (B65.11). It is labelled "*T.huttoni* Hector PL.XVIa Fig.34, *T.arctica* Heer, Arber PL.VI fig.1, *T.daintreei* T.M.H. 1981".

The leaves included in Hector's "unpublished plates" as PL.XV, Fig.8 (B161.5), Fig.11 (B65/16); PL.XVIa, Fig.34 (B65.11, see above), Fig.35 (B65.12) & Fig.41 (B65.15, labelled "*T.huttoni* Hect., *T.daintreei* T.M.H"), all show venation similar to that of Arber's *T.arctica*. All are labelled as being from "Waikato Heads" but all have the matrix characteristic of the Pakawau deposits. In addition nearly every block of N.Z.G.S. collection B74, localised as originating from Pakawau and having the same matrix, clearly bears two taeniopterid species, *T.arctica* and *T.stipulata*. Leaves actually from Waikato Heads (eg. Hector "unpublished plates" PL.XV, Fig.1 (B77.5)) correspond well with leaves from South Island localities which Arber assigned to *T.daintreei* (see Appendix 2.1 for further detail of Arber's species determinations).

Edwards (1934, p. 97) transferred the "Waikato Heads" material which Arber had placed in *T.arctica* to *Taeniopteris spatulata* McClelland. Thus, it would seem that Edwards failed to realise Arber's intention to indicate the likelihood that *T.arctica* was a fern.

Blaschke and Grant-Mackie (1976, p.939) used population studies based primarily on lamina width to distinguish two species of *Taeniopteris*. Leaves from Port Waikato were assigned to *T.daintreei* McCoy. Leaves from Clent Hills were assigned to *T.thomsoniana* Arber which they maintain is the only species occurring there (cf. Ettingshausen 1891, Arber 1917).

It is reasonable that Blaschke and Grant-Mackie discount Arber's use of *T.arctica* Heer for their Port Waikato leaves on the grounds of structure, age and location but the "possible presence of sori" (op. cit., p.936) on *T.arctica* does not preclude its attribution to the form genus *Taeniopteris* (eg. see Edwards 1926, p. 124).

Having correctly pointed out (loc. cit.) "that Arber's (1917) allocation of the Port Waikato population to *T.arctica* was based on a specimen subsequently found to have come from upper Cretaceous strata of Pakawau, Nelson", Blaschke and Grant-Mackie failed to recognise there are two taeniopterid taxa at Pakawau. Furthermore, they incorrectly state that "The New Zealand hypotype of *T.arctica* (from the upper Cretaceous at Pakawau) also fits into the description of *T.daintreei* from Victoria, but population studies allow separate recognition of the Pakawau form as *T.stipulata* (McQueen 1956)." In spite of this statement they include "1917 *T.arctica* Heer: Arber" in their synonymy of *T.daintreei* McCoy.

It is clear that *T.batleyensis* and *T.arctica* are almost certainly synonymous, but revision of the taxa to establish this has not so far been undertaken. Therefore, for the present, *T.batleyensis* is retained for fertile fronds only, while *T.arctica* is applied to infertile fronds with venation density and forking similar to *T.batleyensis*. Only one specimen (CU 412.20 Cl) which may confidently be assigned to *T.arctica* has been found in the middle Clarence valley.

5.3. Results and Discussion

5.3.a. Character Analysis

The fossils used in this study were collected from six localities in the middle Clarence valley. For details of collection and of analysis procedures, see Chapters 2 and 3 respectively. Individual fossils

were allocated to a taxon according to the presence of the characters listed in Table 5.1. Where crucial character combinations were lacking, allocation was by "best guess"; this lack of characters is particularly common for basal-medial fragments. Also, a particular character may show some variation within a taxon. The statistics for the taxa considered are presented in Table 5.2.

Analysis of correlation coefficients shows that lamina width and midrib width are correlated, as are maximum and minimum secondary vein angles.

Stepwise discriminant analysis (SDA) was carried out in two parts.

1. SDA of leaves assigned to the four groups *Taeniopteris stipulata*, *Nilssonia elegans*, *Nilssoniopteris* sp. and "linearphyll" (see Section 3.3.2.a), using the three characters lamina width (W), midrib width (M) and the ratio midrib width/lamina width (M/W) with F-to-enter = 4. This established that "linearphylls" are distinguished from all other groups using M/W and M. The other three groups could not be distinguished from each other.

2. SDA of leaves assigned to the three groups *T.stipulata*, *N.elegans* and *Nilssoniopteris* sp., using the six characters lamina width (W), midrib width (M), the ratio M/W, maximum angle (MAX), minimum angle (MIN) and the difference between maximum and minimum angle (MAX-MIN), with F-to-enter = 2. This established that the three groups are distinguished using MAX and M. MIN serves to distinguish *N.elegans* from the other two groups. MAX-MIN was of no use whatsoever.

It should be noted that the ranges exhibited by individual taxa for these characters overlap (Table 5.2). Thus, although the statistics suggest that it is possible to distinguish taxon means on a population basis, in practice an individual cannot be satisfactorily allocated to a particular taxon using these characters. Thus in the absence of determination using the characters in Table 5.1, the individual should be attributed to *Taeniopteris* sp. indet.

The use of t-tests to compare mean lamina widths showed that, just as one would expect, there is a high probability ($p > 0.05$) that "linearphyll" (Clarence) and *T.daintreei* (Port Waikato) are from different statistical populations. However, similar comparison of *T.stipulata* (Clarence) and *T.thomsoniana* (Clent Hills) showed that there is a high probability ($p > 0.2$) they are statistically from the same population. This suggests that lamina width is not a suitable character for differentiating species (see also Arber, 1917, p.45).

5.3.b. Cuticular Micromorphology

No cuticle was obtained from *T.stipulata* samples suggesting it is absent, thin, or fragmented by rock grain impact.

SEM photos were obtained for *N.elegans* samples (Plate 13A) prepared by the *in situ* method.

Small fragments of cuticle from *Nilssoniopteris* sp. samples were obtained by standard maceration procedures and were examined with the light microscope.

Analysis of cuticular micromorphology is presented in the systematics section.

5.4. Systematics

Class Cycadopsida

Order Pentoxylales

Taeniopteris A. Brongniart 1828 emend. Harris 1932

Taeniopteris stipulata Hector ex McQueen 1956

Synonymy:

1873 unnamed: Hector "unpublished plates" PL.XXVIII, Fig.36,37,41 (Pakawau), Fig.39,40 (Shag Point)

1886b *T.stipulata*: Hector p.61, Fig.24A.3(Pakawau)(name and inaccurate sketch of PL.XXVIII, Fig.37)

1956 *T.stipulata* Hector: McQueen p.683 Text-Fig.3, Figs.4-7 (Pakawau, Quail Flat, Shag Point)
(description and figures)

Lectotype: B161/24, NZGS Coll., Pakawau

Diagnosis: leaf simple, lorate to narrowly elliptic; margin entire or undulate; apex gradually tapering, acute or acuminate, occasionally obtuse; ^{lamina} base very acute, decurrent, tapering gradually and somewhat unevenly; midrib smooth or finely striate, maintaining width upwards, persisting to apex; no distinct petiole; secondary veins usually simple, rarely forking, then only once and always basally.

Material from Clarence included: Horse Flat, 100.06; Alexander McKay Terrace, 212.14, 214.03, 214.04, 214.10; East Quail Flat, 72 specimens including a complete juvenile (330.06); West Quail Flat, 410.24, 411.05, 412.48; Ptilophyllum Ridge, 521.08; lower Seymour Stream, 614.01, 614.03 (3 specimens); upper Seymour Stream, 36 specimens.

Number of specimens from Clarence included: 126.

Plate 12F,G.

Emended Description: leaf simple, lorate to narrowly elliptic, usually straight, occasionally curved, length up to 11 cm (incomplete), width mean 1.5 cm, range 0.85-3.2 cm.; margin entire or undulate; apex gradually tapering, acute or acuminate, occasionally obtuse; ^{lamina} base very acute, decurrent, tapering gradually and somewhat unevenly; midrib smooth or finely striate, strong, width mean 0.12 cm, range 0.07-0.2 cm, maintaining width upwards, persisting to apex; no distinct petiole.

Secondary veins arising from midrib generally close to 80^0 , often different on each side (^{angle (MIN)} minimum _{mean} 73^0 , range 65^0 - 90^0 , ^{angle (MAX)} maximum _{mean} 82^0 , range 75^0 - 90^0), angle not decreasing towards apex, parallel; usually simple, rarely forking, then only once and always basally; frequency at margin mean 36 per cm, range 18-50 per cm.

Discussion: in describing *T.stipulata*, McQueen (1956) made use of 10 specimens in the N.Z.G.S. Collection to establish the distinguishing characters and range of dimensions of the species but did not provide a diagnosis which would serve to distinguish his species from others in the form genus. With the revision of characters which distinguish the New Zealand taeniopterid species of various authors from each other (see Appendix 2 and "Key", Section 5.5), together with the present collection of 35 measured specimens (Table 5.2) from the middle Clarence valley, the previously described characters and

dimensions of *T.stipulata* require amendment. Therefore, an emended description is given to accomodate all specimens which, in the terms of the diagnosis provided, belong in this taxon.

Comparison: *T.stipulata* is distinguished from other New Zealand taeniopterids by its elliptic leaf shape (some *T.daintreei* may approximate) with a more abruptly tapered ^{lamina} base, secondaries generally more acute and more dense but rarely forked and then always basally, and by its occurrence in rocks of Cretaceous age or younger.

Remarks: McQueen (1956 p. 683) placed *T.stipulata* in the order Bennettitales although he had no evidence to justify doing so. It should be noted that the works of later writers (Harris 1962, Blaschke & Grant-Mackie 1976, Drinnan & Chambers 1985) relating leaves of this form to Pentoxylales fructifications were not of course available to him.

The use of *T.stipulata* for taeniopterid leaves from Waikawa by Park (1887) is disputed; they are more properly located in *T.daintreei* (see above and Appendix 2.1).

Large numbers of incomplete leaves occur together in both mudstone ("local") and crevasse splay deposits.

Order Cycadales

Nilssonia Brongniart 1825

Nilssonia elegans Arber 1917

Synonymy:

1873 unnamed: Hector "unpublished plates" PL.VI, Fig.9 (Mataura Falls)

1887 *N.zeelandica*: Ettingshausen p.42 (no figure or description) (Mataura & Waikawa)

1917 *N.elegans*: Arber p.52, PL.VIII, Fig.8 (holotype); PL.IX, Figs.1,3 (name and description) (Mataura Falls)

1934 *N. elegans* Arber: Edwards p.98 (no figure or description) (Waikato Heads)

Holotype: B64.11, NZGS Coll.

Emended Diagnosis: leaf simple, linear, oblanceolate or narrowly cuneate; lamina gradually increasing in width from the base, entire or lobed, indented usually $1/3$, occasionally fully to midrib, lobes of unequal size; apex subacute, bluntly pointed or rounded obtuse; ^{long tapering basal region of lamina} \wedge very acute, decurrent, long, tapering asymmetrically and unevenly; margin sinuate, often indented; midrib maintain^{ing} width upwards, persisting to apex, no distinct petiole; secondary veins prominent, forking usually once near midrib.

Other material from Clarence included: Horse Flat, 25 specimens including a complete juvenile (123.03); Alexander McKay Terrace, 220.08; East Quail Flat, 330.37, 330.48, 330.52 (3 specimens), 330.53; upper Seymour Stream, 732.09, 732.21, 732.27, 732.42 (2 specimens).

Number of specimens from Clarence included: 37.

Plates 12A&B, 13A

Emended Description: leaf simple, linear, oblanceolate or narrowly cuneate, lamina gradually increasing in width from the base, length up to 16 cm., width mean 1.8 cm., range 0.5-3.5 cm.; lamina entire or lobed, indentation usually $1/3$, occasionally fully to midrib, lobes of unequal size, apical edge 90^0 to midrib, straight, lower edge 45^0 to midrib, straight; substance of lamina of medium thickness; apex subacute, bluntly pointed or rounded obtuse; ^{long basal region of lamina} \wedge very acute, decurrent, long, tapering asymmetrically and unevenly; margin sinuate, often indented; midrib strong, width mean 0.15 cm., range 0.07-0.25 cm., maintain^{ing} width upwards but may reduce slightly in upper part, persist^{ing} to apex, straight; no distinct petiole.

Secondary veins prominent, fine, set at 60^0 - 80^0 to midrib, often different on each side (^{angle (MAX)} maximum \wedge mean 71^0 , ^{angle (MIN)} minimum \wedge mean 65^0) parallel, sometimes initially arched; typically at a density of 24 per cm. at midrib, 40 per cm. on lamina, forking usually once near midrib, some end in margin of indentation, some curve round indentation to end in distal margin of lobe.

Cuticle of lower surface thin, interveinal cells irregular, anticlinal flanges straight to irregular, 3.6 μm thick; stomata ^(See Addenda)haplocheilic, probably transverse; probably ~~is~~ subsidiary cells lacking strongly cutinised ledge between guard cells and subsidiary cells; stomatal aperture 70 μm .

Discussion: Arber had only six leaves from which to describe *N.elegans*. Indeed, that is still the extent of the N.Z.G.S. collection (B.64.7, 64.10, 64.11) of the species from Mataura Falls. The largest of these leaves is 10 cm. (incomplete) long and 0.9 cm. wide with secondary veins set at 65^0 - 70^0 to the midrib. These dimensions fall within the range for 24 measured leaves (Table 5.2) from the middle Clarence valley believed to be conspecific with *N.elegans* Arber. Other ^{available} characters are in sufficient accord with Arber's diagnosis that, in spite of the age difference, erection of a new species is considered unwarranted. However, in view of the increased character ranges it is considered desirable to emend his diagnosis and description. It should however be noted that although cuticular studies have confirmed the appropriateness of the attribution of the Clarence material to *Nilssonina*, now accepted (cf. Harris 1964) as a cycadalean genus, no such information and confirmation is available for any of the Jurassic material described by Arber as *N.elegans* (from Mataura Falls), or so attributed by Edwards (from Waikato Heads).

Comparison: Harris (1964, p. 32) states that in *Nilssonina* Brongniart the veins are simple. The veins in the Clarence fossils fork and Arber (1917 p. 52), referring to the Mataura fossils, says they "no doubt occasionally fork". This suggests the New Zealand fossils should not be included in *Nilssonina* until supported by reproductive structures even though all other ^{available} characters are in agreement. However cuticular micromorphology is in agreement with that described by Harris, therefore the generic determination is retained. Using the key to "Yorkshire sp. of *Nilssonina*" (Harris 1964, p. 32) the present fossils would key to *N.sp A*.

Douglas (1969 p. 62) described several "*Taeniopteris*-like leaves with serrate and lobate margins". The only one which approaches *N.elegans* is Type 2 (Figs. 1, 69) but the indentations are V shaped and the leaf commonly narrower (less than 1.5 cm).

Douglas (loc.cit.) also describes *T.sp."C"*. The leaf illustrated in PL.19, Fig.1 has similar venation to *N.elegans* and he remarks (p.25) that it "might well represent *Nilssonina* sp.". However the description and outline (p.62, Figs.1,63-64) are quite different.

Bell (1956, p.103, PL.47, Fig.5, PL.49, Figs.3,6) described *Nilssonina nigracollensis* Wieland from western Canada. It is similar to *N.elegans* but is smaller (up to 7 cm. or more long, 0.2-1.0 cm. wide), has a midrib only 0.1 cm. wide, is entire margined or rarely cut almost to the rachis into obtuse segments. It has secondary veins at a density of 18-30 per cm. which are simple or rarely forked near their point of origin, are set at 50° - 80° to the midrib, and slightly curve towards the apex. The apex is obtuse or narrowly rounded. It occurs only in the Neocomian.

Remarks: Ettingshausen (1891,p.242) referred to *Nilssonina zeelandica* from Mataura and Waikawa but provided no description or figure. It is here presumed to correspond to *N.elegans* Arber.

None of the fossils figured in Hector's "unpublished plates" clearly represent *N.elegans*. However specimen B64.11 in the NZGS collection (Arber's holotype) has a label indicating it is Hector's unpublished plate PL.VI, Fig.9 and the outline (except that it lacks lobes) does indeed correspond to a leaf on the specimen.

The presence of a simple-leaved cycad in both the Mataura Falls (Jurassic) and Clarence valley (Cretaceous) floras is accompanied by the occurrence of the pinnate-leaved cycads *Nilssonina compta?* at Mokoia (Arber 1917, p.51) and *N.pseudocompta* sp.nov. in the Clarence valley (see Chapter 6).

In the middle Clarence valley, small numbers of leaves, generally long though not complete, occur scattered in crevasse splay deposits. In the upper Seymour Stream, they occur in tuff.

Order Bennettitales

Nilssoniopteris Nathorst 1909 (Diagnosis Harris 1969)

Nilssoniopteris sp.

Type: CU 100.05 CL.

Collection: J.D.Lovis et.al., Horse Flat, Dec. 1978.

Other material included: Horse Flat, 100.01, 100.03 (complete juvenile), 100.05, 100.12, 100.15 (two apices), 100.17 (basal 2/3 plus three fragments), 100.29, 122.11 (many fragments); East Quail Flat, 330.16; Quail Flat (collected by A.McKay, 1885) B125/37A, counterpart B166/10.

Number of specimens included: 12.

Plate 12E.

Description: leaf simple, elliptic to oblanceolate, of varied size up to 9.8 cm long and 2.4 cm wide, middle region of even width, ~~apical and basal regions~~ somewhat narrowed; apex rounded obtuse, tapering gradually in top 1/5 but rapidly in top 1/20; ^{lamina} base acute 45° , tapering more or less quickly, lamina ending abruptly or slightly decurrent on petiole, always contracting and ending unequally; substance of lamina thin, flat, attached laterally, margin entire, not recurved; midrib smooth, somewhat curved, broad below, 0.15-0.22 cm., narrow above, decreasing upwards soon after leaving petiole and not persisting to apex; petiole short, stout, without wrinkles, base perhaps expanded.

Secondary veins conspicuous in hand specimen, straight, meeting margin, set at mean 76° , range 70° - 80° to midrib but near apex angle to midrib decreasing and veins curving *apically*; arising at a density of approximately 24 per cm., simple or occasionally once forked, forking basal or (rarely) further out.

Discussion: Cuticle preparations indicate that there were epidermal cells with slightly sinuous walls, and probably syndetochelic stomata with a strong ledge between guard and subsidiary cells. One specimen

has 40 μm diameter "resin bodies" in the lower epidermis. These characters suggest it is a bennettite, but a literature search (not yet completed) has failed to reveal a species to which these leaves may be referred.

The smallest leaf found (Plate 6B, to the left of the white square) is oblanceolate, 3.0 cm long and 0.9 cm wide, with an obtuse apex and tapering base. While these characters suggest this leaf would be better placed in *Nilssonia elegans*, its midrib and secondary vein pattern place it clearly in the present taxon.

The similarities between these fossils and those assigned by Arber to *Taeniopteris crassinervis* (Feistmantel) Arber (see Appendix 2.1) are considerable. Details of venation pattern, apex shape, distinctively contracted ^{lamina} base, midrib not persisting to the apex and complete margin are all in agreement for the two taxa. *T. crassinervis* differs (albeit very considerably) from *Nilssoniopteris* sp. only in leaf size (8-19 cm long and 1.5-8 cm wide), midrib width (up to 1 cm), vein dimensions (0.5 mm across, 8-12 per cm), and age (Jurassic). Leaf size is discounted by Arber (1917 p.45) as a useful distinction between *Taeniopteris* and *Macrotaeniopteris*, to which *T. crassinervis* had been referred by Hector, and is similarly discounted here. However the specific name of the Jurassic species has such significance in relation to the venation dimensions, it is felt unwise to assign the present fossils to that taxon. Therefore, a new species is here proposed for Cretaceous leaves with less massive midrib and secondaries. Furthermore, since cuticular studies suggest *Nilssoniopteris* sp. may be established (admittedly shakily) as a bennettite, it is further proposed that the generic attribution of *T. crassinervis* should be revised to *Nilssoniopteris* Nathorst, based on the overall similarity of the two taxa.

Comparison: *Nilssoniopteris* sp. is distinguished from other N.Z. taeniopterid leaves, apart from *T. crassinervis*, by its thin lamina ending abruptly and unevenly basally, and by the midrib diminishing apically and not persisting to the apex. It occurs in the middle Clarence valley with both *T. stipulata* and *Nilssonia elegans* which have secondary veins at greater (the former) or lesser (the latter) angles to the midrib. When the medial portion of a leaf is the only portion preserved it is very difficult to distinguish the three, but *T. stipulata* has an elliptic shape with gradually tapering base, and *N. elegans* ^{often} has notched margins.

Nilssoniopteris vittata (Harris, 1969) has linear lanceolate leaves up to 25 cm long (length 10x width), small leaves linear with apex tapering acute, lamina thick, veins inconspicuous above, moderate below at a concentration of 12-24 per cm and margin recurved, thick apparently entire.

Nilssoniopteris major (Harris, 1969) is a much larger leaf and has minute teeth on the margin.

Nilssoniopteris pristis (Harris, 1969) has obvious teeth on the margin.

Remarks: McQueen (1955,p.683) included under *T.stipulata* the N.Z.G.S. collection specimen B125.37. The block bears three marked leaves,"A" and "B" on the labelled surface, and "C" on the back. "A" is here included in *Nilssoniopteris* sp. "B" and "C", together with several unmarked leaves, are indeed *T.stipulata*.

Very few, but usually complete, leaves occur scattered in both mudstone and crevasse splay deposits.

5.5. Conclusions

Given preservation of a sufficient portion of the leaf, taeniopterids from New Zealand Jurassic strata may be attributed to one of four species, *Nilssonia elegans*, *Taeniopteris crassinervis*, *T.daintreei*, or *T.thomsoniana* (see Appendix 2.1). Those from Cretaceous strata may be attributed to one of five species, *Nilssonia elegans*, *Nilssoniopteris* sp., *Taeniopteris stipulata*, *T.arctica*, or *T.batleyensis*. *T.arctica* probably represents the infertile fronds of *T.batleyensis*. Where insufficient leaf is preserved, it is best attributed to *Taeniopteris* sp. indet.

A specific determination is sufficient to be able to assign a leaf to the pteridophyte *T. batleyensis* or to one of three orders of gymnosperm which have been determined by association (Pentoxylales) or by cuticular micromorphology (Cycadales and Bennettitales).

Pentoxylalean leaves (*T.daintreei*, *T.thomsoniana*, *T.stipulata*) are long, narrow, entire with a tapering decurrent base, scarcely petiolate and with thin cuticle (not so far found preserved). They are apparently deciduous, occurring as "leaf banks".

Cycadalean (*Nilssonia elegans*) leaves are simple and long, gradually expanding upwards from an apparently apetiolate base, with a lamina lobed by indentation of the margin. Their cuticle, while thin, is preserved. They are unlikely to be deciduous and do not occur as "banks".

Bennettitalean leaves (*Nilssoniopteris* sp., *T. crassinervis*) which are simple (see Chapter 6 for pinnate bennettites), have an abruptly expanded lamina with a strong petiole and midrib, the latter diminishing upwards and not extending to the apex. Their cuticle is thin and poorly preserved. They appear to be deciduous or at least fall from the stem when mature (commonly whole leaves are preserved).

It would appear likely that two sets of species of New Zealand taeniopterids exist which, with discovery of fructifications, may be reduced to chronospecies. *T. daintreei* is the most probable ancestor of *T. stipulata* in view of the general leaf shape and its wide distribution (see McQueen 1956 p. 675). *Nilssoniopteris* sp. may be a direct descendant of *T. crassinervis*, each being the only simple-leaved bennettite species occurring in their respective ages.

Key to New Zealand Jurassic and Cretaceous Taeniopterids

- | | |
|--|---|
| 1(a) ^{Lamina} base long, acute, decurrent (or base absent). | 2 |
| (b) ^{Lamina} base suddenly contracted to petiole. | 5 |
| 2(a) Margin entire, midrib persisting to apex. | 3 |
| (b) Margin entire, midrib not persisting to apex. | 5 |
| (c) Margin indented at least 1/3 to midrib. | |

Nilssonia elegans

- | | |
|--|---|
| 3(a) Leaf shape linear oblong or elliptic. | 4 |
|--|---|

- (b) Leaf shape oblanceolate

Taeniopteris thomsoniana

- (c) Leaf shape cuneate

Nilssonia elegans

- 4(a) Leaf linear oblong, secondary vein density 15/cm,
forked (U-shaped) once, usually basally.

Taeniopteris batleyensis

- (b) Leaf linear oblong, secondary vein density 15-30/cm,
mostly forked (V-shaped) once, occasionally twice.

Taeniopteris daintreei

- (c) Leaf elliptic, secondary vein density 18-50/cm,
rarely forked, always basally.

Taeniopteris stipulata

- 5(a) Leaf large, midrib broad, secondary veins stout
(0.5 mm across), at 8-12/cm.

Taeniopteris crassinervis

- (b) Leaf moderate or small, midrib moderate, secondary veins
moderate, at 24/cm.

Nilssoniopteris sp.

6.1. Introduction

The fossil leaves collected from the study area which are pinnately compound with parallel secondary veins (Plates 12,14,16,17) (but excluding those fossils superficially resembling such pinnate leaves, which are here interpreted as "juvenile" *Agathis* foliage spurs, Plate 24B,F), are assigned to nine form species. Three species of pinnate-leaved cycadophytes ^(see Addenda) had been reported previously by McQueen (1956), *Zamites* cf. *takuarensis* Walkom (now however believed to be a species of *Agathis*, see below), *Ptilophyllum seymouricum* McQueen and *Pterophyllum clarencianum* McQueen.

Seven new species are described here. One, *Nilssonia pseudocompta*, belongs in the Cycadales while the remainder, *Otozamites* sp., *Anomozamites blechnoides*, *Pterophyllum rectipinnatum*, *P.sp.A*, *P.sp.B*, and *P.sp.C* belong in the Bennettitales. New material allows the description of *P.seymouricum* to be emended. One simple-leaved member of each of the Cycadales, (*Nilssonia elegans*), and the Bennettitales, (*Nilssoniopteris* sp.), also occur in the Clarence flora, but since both correspond to the form genus *Taeniopteris*, they were considered in Chapter 5.

6.2. Taxa Previously Described from the Clarence Area

D.R.McQueen (1956,p.682), under the order Cycadales, described and figured *Phyllopteris lanceolata* Walkom (Text-fig.2, fig.13) from the Ford Formation of the Paparoa Coal Measures, *Phyllopteris expansa* Walkom (Text-fig.2, figs.10-12) from Quail Flat and Brunner Bridge, and *Zamites* cf.*takuarensis* Walkom (Text-fig.3, fig.11) from Coverham. *P.lanceolata* and *P.expansa* were transferred to the genus *Phyllopteroides* by Medwell (1954) and are now considered to be osmundaceous (Cantrill and Webb, 1987) They were discussed in Chapter 4.

With regard to the fossils placed by McQueen in *Zamites*, it should be noted that Coverham lies 50 km. N.E. of Quail Flat, but within the "Kaikoura" Cretaceous inlier. The beds there are marine, and the fossils in question must have been transported some distance. Examination of the two specimens

involved, B470/1 (Plate 24C) and B470/2 in the N.Z.G.S. Collection reveals that the impressions, because they lack coaly material, show rather poor contrast and are difficult to interpret. In my opinion, the apparently spiral phyllotaxis of the slightly petiolate leaves suggest they are not cycadophyte, but foliage spurs of *Agathis*, most probably conspecific with *A.seymouricum* sp.nov., described in Chapter 8.

Under the order Bennettitales, McQueen (1956) described and figured *Pterophyllum clarencianum* n.sp. (loc.cit.p.684, Text-fig.3, fig.10) from Quail Flat, and *Ptilophyllum seymouricum* n.sp. (loc.cit.p.685, Text-fig.3, figs.8,9) from Seymour Stream. The former is based on a single indifferently preserved specimen (see Plate 16E) which makes satisfactory comparison of other fossils with it difficult; therefore the collection is left in isolation. The latter is here emended because further collecting has shown the original material to be atypical.

6.3. Systematics

Class Cycadopsida

Order Cycadales

Nilssonia Brongniart, 1825, p.200.

Nilssonia pseudocompta sp.nov.

Holotype: CU 121.14b Cl.

Collection: Horse Flat, I.L.Daniel and J.D.Lovis, Jan.1986.

Diagnosis: leaf pinnate, linear to oblanceolate, apex obtuse, ^{lamina}base acute decurrent, tapering gradually, margin indented, dividing lamina into triangular to rhomboid lobes; lobes alternate below, sometimes opposite above, length increasing *apically*, width approximately constant except for occasional *undivided* lobes, usually set at 80° to rachis, ^{lobes}apex usually truncate but acute in basal triangular lobes;

indentation between lobes regular, round to acute, asymmetrical; veins obscure, arching round indentation, then running nearly parallel to lateral margins and meeting distal margin, at about 20 per cm. in middle of lobe, rarely dividing once and then only near rachis, usually 14-16 (occasionally 20) per lobe.

Other material included: Horse Flat, 100.25 (juvenile), 121.11, 121.13, 123.04.

Plates 12C&D, 13B.

Derivation: from *pseudo* - Latin meaning false, and *compta* the Jurassic species.

Description: leaf pinnate, linear to oblanceolate, length (incomplete) 19 cm., width in middle or *apical regions*, 3 (-4)cm.; apex more or less obtuse, *with possibly* mucronate apical pinna, at least in "juveniles"; *lamina* base acute, decurrent, tapering gradually to petiole; petiole length and base unknown; margin indented, dividing lamina into lobes; rachis stout 0.22 cm., narrowing *apically*, persisting to apex, straight, with three to four grooves.

Lamina thick, obviously continuous ^{on rachis but} usually cut almost to rachis but occasionally to one third distance from rachis to margin, divided into triangular or, more commonly, rhomboidal lobes. Lobes alternate *basally*, sometimes opposite *apically*, often of very uneven dimensions, length 0.5 - 1.5 cm. (rarely up to 2 cm.) increasing *apically*, width 0.5 - 1.0 cm., approximately constant *apically* except for occasional *undivided* segments, length to width ratio 1.0:1 - 1.5:1, commonly as broad as long in *basal* part of leaf, but *lobes* becoming longer than broad ^{apically}, set at 65^0 - 90^0 to rachis (usually at 80^0), *apical* margin straight to slightly convex at 90^0 to rachis, *basal* margin concave before sloping forwards at 45^0 or more to rachis, curving *apically* and continuing without a break into the distal margin, apex usually truncate but acute in basal triangular lobes. Indentation between lobes regular, round to acute, asymmetrical.

Veins obscure, buried within lamina, arising from rachis at 80^0 , arching round indentation, those arising below a lobe arching ^{apically} more than those arising above a lobe arch ^{basally}, all then running nearly parallel to lateral margins and meeting distal margin; at about 17 per cm. near rachis, 20 per cm. in middle of lobe; rarely dividing once and then only near rachis, usually 14-16 (occasionally 20) per lobe.

Cuticle thin, trichomes on *adaxial* surface, ?amphistomatic; stomata scattered, aperture 30 μ m., with 5-6 ^c _Λ *stomatocytic* subsidiary cells, lacking a strong ledge between guard and subsidiary cells.

Discussion: leaves have never been found whole, basal fragments being the most common. These are similar to the basal fragments of *N.elegans* but the latter lack the regular lobation of *N.pseudocompta*. The holotype appears to have been broken distally during life and bears a small lobe on either side of the rachis suggesting regrowth after injury. The "juvenile" leaf (CU 100.25 CI) suggests that lobation is irregular in the early stages of leaf growth and that lobes do not themselves elongate as the leaf grows, i.e. as "development proceeds from the base upwards, each pair of [lobes ceases to grow] ... as soon as that part of the rachis has attained its full degree of extension and size" (adapted from Morris, 1841, p.111, on the development of modern *Cycas* leaves).

Comparison: the leaves from the N.Z. Jurassic doubtfully attributed to *N.compta* (Phillips) Brongniart by Arber (1917) and Edwards (1934) closely resemble *N.pseudocompta*, showing both "juvenile" and "adult" forms.

Of the nine species of *Nilssonia* described by Harris (1964) from the Yorkshire Jurassic, only *N.compta* and *N.kendalli* resemble *N.pseudocompta* in general leaf form. *N.compta* has generally larger leaves 50 cm. long and 4(-6) cm. wide, with broad, projecting veins which tend to curve forward at the distal margin. *N.kendalli* has smaller leaves 15 cm. long and 2-4 (typically less than 1) cm. wide, with much more crowded veins (35 per cm. at the rachis).

Harris (loc.cit. p.54) points out that "Many specimens figured from other floras look more or less like *N.compta* and *N.kendalli*, but where fine details have been described there are differences. The question whether such specimens, whether determined as *N.compta* or given other names, are identical with Yorkshire *N.compta* must be left until they are re-examined". In view of this, and of the wide temporal and geographical separation of the present fossil (*N. pseudocompta*) from admittedly very similar taxa, it is felt best, at this stage of the investigation, to erect a new species. The eventual preparation of good cuticle samples and/or discovery of reproductive organs may or may not prove this to be well founded.

Anomozamites Schimper, 1870, p.140

Anomozamites blechnoides sp. nov.

Holotype: CU 742.23 Cl

Collection: I.L.Daniel and J.D.Lovis, upper Seymour Stream, Feb, 1985.

Diagnosis: leaf pinnate, linear; rachis straight, showing faint striations but not transversely wrinkled; lamina attached laterally, indentations round, symmetrical, usually almost to the rachis, occasionally to half way; pinnae broadly triangular, usually subopposite, occasionally alternate, apex rounded obtuse, attached by whole base, base not contracted, margin entire; veins obvious, parallel or converging, ~~apical veins of~~ ^{basal veins of} ~~a lobe~~ not curving round indentation, ~~a lobe~~ ^{curve} slightly, 25-40 per cm., 7-10 per pinna; cuticle showing square epidermal cells with slightly sinuous walls, stoma with two paracytic subsidiary cells with nearly semicircular, not sinuous, outer walls.

Other material included: upper Seymour Stream, 712.47, 742.31, 742.55 (two specimens).

Plates 14A&B, 15A-C.

Derivation: from *Blechnum*, the fern genus, and *oides* - Greek, indicating resemblance.

Description: leaf pinnate, linear, length (incomplete) 8 cm., width 1.3 cm. below to 1.8 cm. above; apex and base unknown; rachis straight, 0.2 cm. wide, showing 4 faint striations but not transversely wrinkled; lamina apparently attached laterally, indentations round, symmetrical, usually almost to the rachis occasionally to half way; petiole unknown.

Pinnae broadly triangular, usually subopposite, occasionally alternate, length 0.5-0.7 cm., width at base 0.5 -0.7 cm.; apex rounded, obtuse, attached by whole base; base not contracted; axis of pinnae at 65° to rachis on one side and 100° on other; ~~apical~~ margin at 80° - 115° to rachis, ~~basal~~ margin at 65° - 90° to rachis, convexity of ~~basal~~ margin greater than that of ~~apical~~ margin, margin of pinnae entire.

Veins obvious macroscopically but not clear microscopically, arising at 65^0 or 100^0 (same as main axis of pinnae) to rachis, forking pattern unknown, parallel or converging, meeting margin acutely, apical veins - not curving round indentation, ^{basal} veins curve slightly; 25 - 40 per cm., 7 - 10 per pinna.

Cuticle of ^{abaxial} epidermis ^(Plate 15 A, B) showing cells square or less regular with slightly sinuous walls; one stoma with aperture $30\text{ }\mu\text{m.}$, guard cells with margin next to stomatal opening thickened and crescent-shaped dorsal thickening; two paracytic subsidiary cells rather small but extending beyond guard cells, outer wall nearly semicircular, not sinuous.

Cuticle of ^{abaxial} surface of rachis ^{(Plate 15 c) thick} medium, cells in rows, rectangular and polygonal, $24\text{ by }22\text{ }\mu\text{m.}$, intercellular flanges $3.7\text{ }\mu\text{m.}$

Discussion: although based on only one clear specimen, less well preserved specimens and separated pinnae have also been used to allow good specific definition. It is clearly different from any other leaf occurring in the area. The different angle of pinnae on either side of the rachis is most likely a preservational effect.

Comparison: the generic determination follows that of Harris (1969, p.79) when he states "the sole distinction from *Pterophyllum* is in the shape of the lamina segment which in *Pterophyllum* are typically much longer than broad".

Of species described by Harris (loc.cit.), only two show similarity. *A.nilssoni* (Phillips) has a wider leaf, square or rhomboidal pinnae with 15 veins per segment and dentate margin. *A.thomasi* Harris has a rachis with transverse wrinkles, and rectangular segments which overlap and are set at 80^0 to the rachis. The cuticle of the latter has moderately sinuous anticlinal flanges and a ridge round the stomatal aperture forming a rectangle.

Pterophyllum Brongniart, 1828, p.25.

Pterophyllum clarencianum McQueen, 1956, p.684, Text-fig.3, Fig.10.

Holotype: B166/60, N.Z.G.S. Coll.

Description: as given by McQueen, 1956.

Discussion: this taxon is based on a single specimen (Plate 16E) collected by McKay in 1885 at "Quail Flat" (precise location unknown). The holotype is a poor impression with ill-defined pinnae, margin and venation, thus making satisfactory comparison of other fossils difficult. No information is available about cuticular structure. The species described below (*Pterophyllum* sp. C) may be conspecific, but the match is not exact and therefore this collection is left in isolation within the *Pterophyllum* complex to which it undoubtedly belongs.

Pterophyllum sp.C.^P(^Acf.*clarencianum*).

Type: CU 120.01 Cl.

Collection: I.L.Daniel and J.D.Lovis, Feb, 1985.

Other material included: Horse Flat, 100.15; Alexander McKay Terrace, 214.16, East Quail Flat, 330.02; Upper Seymour Stream, 740.05, 742.44, 742.45.

Plate 16C&H.

Description: leaf pinnate, linear, length (incomplete) 5 cm., width 3cm; apex and base unknown; margin indented; rachis 0.15 cm.^{proximally,} narrowing ^{distally,} straight with faint medial groove; lamina thin, attached laterally.

Pinnae irregularly placed, alternate and opposite, often ^{undivided} for short distance, gap between pinnae much less than pinna width; length 1.5 cm., width irregular 0.5 - 1.0 cm., occasionally more than 1

cm.; set at 90^0 to rachis; slightly tapering to rounded obtuse, sometimes truncate apex; bases contiguous; ~~apical~~ edge straight, at 90^0 to rachis, edge straight, at 80^0 - 90^0 to rachis, indentation irregular, round, symmetrical, usually reaching to rachis.

Secondary veins obvious macroscopically but not clear microscopically, depart at 90^0 to rachis; ~~apical~~ veins arch down, ^{basal} veins arch up, then parallel to each other and meeting the margin; at a concentration of 24 per cm. at rachis, 30 per cm. at margin; simple or rarely forking once near rachis; 14 - 24 per pinna depending on width of pinna.

Cuticle from ~~adaxial~~ surface thin, interveinal cells elongate rectangular, mean length $68.6\ \mu\text{m}$., mean width $36.9\ \mu\text{m}$.; in rows; anticlinal flanges straight, $<2\ \mu\text{m}$. wide.

Discussion: seven specimens have been found so far. All are fragments of an apparently long, fragile leaf usually with pinnae apices apparently broken or worn off. Their visual similarity to *P.clarencianum* is due in part to the worn state of the leaves prior to preservation. While this condition, unique among the cycadophytes in the middle Clarence valley, may suggest some relationship, there is insufficient correlation of characters to allow positive identification with McQueen's species. Conferring of a specific epithet is deferred until better material is obtained.

Comparison: only three other N.Z. taxa have pinnae set at right angles to the rachis. *P.matauriensis* from the N.Z. Jurassic has a wider rachis, longer more regular pinnae seldom fused, and secondary veins more widely spaced.

P.rectipinnatum (see below) has pinnae regularly spaced along the rachis, a gap between pinnae equal to pinna width and a length/width ratio of 5:1 - 10:1. *Anomozamites blechnoides* (see above) has ~~inately triangular~~ pinnae regularly placed along the rachis, length/width ratio of 1:1 and secondary veins not curving round indentations.

Pterophyllum rectipinnatum sp.nov.

Holotype: CU 123.07 Cl.

Collection: I.L.Daniel and J.D.Lovis, Horse Flat, Feb, 1986.

Diagnosis: leaf pinnate, elliptic, apex acute, base long tapering, margin indented to rachis, rachis straight, with several faint grooves; pinnae opposite to alternate, tapering, length increasing upward to middle of leaf then decreasing to apex, width constant up leaf, apex rounded, acute, base expanded and contiguous with adjacent bases, set at 90^0 to rachis, gap between pinnae equal to pinna width, indentations regular, round, symmetrical, almost to rachis; secondary veins obvious, depart at 90^0 to rachis, ^{apical}veins arch down and ^{basal}veins arch up to curve markedly round indentation, then parallel to each other, meeting margin acutely, 11 per cm. at rachis, simple or occasionally forked at rachis, 6 - 13 per pinna; stomata transverse and oblique, scattered.

Other material included: Horse Flat, 120.18, 121.11(1), 121.13(1&2) (juvenile apex), 122.11, 123.06, 123.07, 123.25; East Quail Flat, 330.13; upper Seymour Stream, 700.02, 700.11(S.E.M.stubs 5,13,82,129), 712.13, 718.27, 740.03, 740.06, 740.07, 742.37 (apex), 742.41, 742.46, 751.08.

Plates 14D&E,15D-F.

Derivation: from *recti* - Latin meaning at right angles, and *pinnatus* - Latin, meaning a leaflet, referring to the pinnae being set at right angles to the rachis.

Description: leaf pinnate, elliptic, length (incomplete) 17cm., width at base 1 cm.; apex acute; base long, tapering; margin indented to rachis; rachis straight, with several faint grooves, width 0.2 cm. ^{proximally,} 0.1 cm. ^{distally,}; lamina thick, attached laterally; petiole long, strong.

Pinnae tapering, opposite to alternate, length 0.3 - 3 cm. increasing upward to middle of leaf then decreasing to apex, width 0.3 - 0.5 cm. constant up leaf; apex rounded, acute, ^{apical} angle more acute than ^{basal}, base expanded and contiguous with adjacent bases; set at 90^0 to rachis; ^{apical} margin concave then straight, ^{basal} margin decurrent, concave then convex; gap between pinnae equal to pinna width, indentations regular, round, symmetrical, almost to rachis.

Secondary veins obvious and clear, depart at 90^0 to rachis, ^{apical}veins arch down and ^{basal}veins arch up

to curve markedly round indentation, then parallel to each other, meeting margin acutely; 11 per cm. at rachis, 22 per cm. at margin (30 per cm. when forked), simple or occasionally forked at rachis, 6 - 13 per pinna.

Cuticle of ^{of} ~~abaxial~~ ^{thickness} surface medium, interveinal cells elongated rectangular; mean length 71 μm ., mean width 19 μm .; anticlinal flanges straight, perhaps pitted, approximately 4 μm . thick; stomata transverse and oblique, scattered, aperture up to 63 μm .; two paracytic subsidiary cells, ledge between guard and subsidiary cells strong.

Discussion: fossils of this taxon found in crevasse splays are large, mature and generally of basal and medial parts of the leaf. Those found in tuffaceous "local" deposits are generally small and include the apical part of a leaf which appears to be rather delicate. The pattern of occurrence of these fossils suggests that the plant was deciduous.

Comparison: *P.matauriensis* has pinnae alternate, rarely subopposite, with obtuse bluntly rounded apices, but is of similar dimensions. *P.clarencianum* and *P.sp.C* have irregular pinnae with gaps between pinnae less than pinna width and L/W ratio 1.3:1 - 3:1. *Anomozamites blechnoides* has much shorter pinnae with L/W ratio 1:1 and secondary veins which do not curve round the indentation between pinnae.

Remarks: *P.rectipinnatum* is the most likely direct descendant of *P.matauriensis* among the Clarence *Pterophyllum* species.

Pterophyllum sp. A.

Type: CU 100.25a Cl.

Collection: J.D.Lovis et.al., April, 1979.

Other material included: Horse Flat 100.27; upper Seymour Stream, 742.32, 751.15a.

Plate 16A,B&F.

Description: leaf pinnate, linear/elliptic, length (incomplete) 9 cm. width 3 cm.; apex of apical pinna obtuse; base unknown; margin indented to rachis; rachis 0.1 cm. below narrowing ~~distally~~, straight except near apex, smooth; lamina thin, attached laterally.

Pinnae usually subopposite, occasionally alternate; length 1.8 - 2.5 cm. width 0.5 - 0.8 cm., slightly tapering; apex often bifid, rounded, acute, or truncate with ~~apical~~ angle more acute than ~~basal~~; base expanded; set at 65^0 to rachis in middle of leaf, 45^0 near apex; ~~apical~~ margin concave to straight, ~~basal~~ margin decurrent then convex, curving ~~apically~~; gap between pinnae less than pinna width, indentation round, very acute, asymmetrical, nearly to rachis.

Secondary veins obvious or perceptible macroscopically but not clear microscopically, depart at 60^0 - 70^0 to rachis; with slight ~~apical~~ arch from rachis then straight and parallel, ~~basal~~ veins meeting ~~basal~~ margin; veins not curving round indentation; 20 per cm. at rachis, 24 per cm. at apex, simple, 6 - 13 per pinna.

Cuticle of ~~adaxial~~ surface thin, interveinal cells elongated, rectangular, in rows, anticlinal flanges straight, thin; with 5-6 cells forming trichome base $97\ \mu\text{m}$ in diameter; stomata ?oblique, solitary, two paracytic subsidiary cells, ledge between guard and subsidiary cells strong.

Cuticle of ~~abaxial~~ surface thin, interveinal cells elongated rectangular, mean length $41\ \mu\text{m}$. mean width $26\ \mu\text{m}$.; anticlinal flanges straight, $2.3\ \mu\text{m}$ thick; stomata solitary or perhaps in rows, two paracytic subsidiary cells, ledge between guard cells and subsidiary cells strong, stomatal aperture $28.75\ \mu\text{m}$.

Comparison: only two other Clarence taxa have pinnae set at other than 90^0 . ~~Apical~~ portions of *N.pseudocompta* have pinnae at 80^0 to the rachis with obscure secondary veins arching round a rounded indentation which often does not reach the rachis. *Pterophyllum* sp.B (see below) has rhomboid pinnae set at 45^0 to the rachis with obvious secondary veins, 10 per cm., not arching round a rectangular indentation.

Remarks: only four specimens have been found which can be confidently assigned to this taxon and the nature of and variation between them precludes a specific epithet being applied at this stage. Also, the cuticle is poorly preserved and its description highly interpretative. However the specimens are sufficiently distinct from other species to require separate description.

Pterophyllum sp.B.

Type: CU 100.32 Cl.

Collection: J.D.Lovis et.al., Horse Flat, April, 1979.

Other material included: Horse Flat, 100.04, 100.05, 100.17.

Plate 16D&G.

Description: leaf pinnate, fragment with one pair of pinnae, length (incomplete) 2.5 cm., width 3 cm.; apex and base unknown; margin indented almost to rachis; rachis only 0.1 cm. wide but strong, smooth, straight; lamina ^{of} ^{thickness} medium attached laterally.

Pinnae rhomboid, subopposite, length 2 cm., width 1.5 cm.; tapering slightly to rounded obtuse apex; base slightly expanded, decurrent; set at 45^0 to rachis; ~~apical~~ ^{apical} edge slightly convex, at 45^0 to rachis, ~~basal~~ ^{basal} edge slightly convex, at 50^0 to rachis; gap between pinnae much less than pinna width, indentation rectangular, almost to rachis.

Secondary veins obvious and clear, depart at 45^0 to rachis, parallel; meet margin at acute angle, often at minor serration; do not curve round indentation; 6 per cm. at rachis, 10 per cm. on lamina; simple or occasionally forking at or near rachis, very occasionally ^{anastomosing}; 13 - 14 per pinna beyond forking.

Cuticle ~~insufficiently~~ ^{well} preserved for description.

Comparison: *N.pseudocompta* has pinnae at 80^0 to the rachis, apex truncate, secondary veins obscure, density perhaps 20 per cm. *P.sp.A* has pinnae set at 45^0 - 65^0 to the rachis, apex acute or truncate, upper edge concave and secondary veins 24 per cm.

Remarks: only one fossil, the type specimen, shows pinnae ^t attached to the rachis, and even this fragment possesses only one pair of pinnae. Three isolated fragments of the apical portion of pinnae show the characteristic vein spacing. A similar apical fragment (specimen CU 412.11a Cl) has veins spaced at 6 per cm. and may, in the future, be placed in this taxon if new material shows variation sufficient to accommodate it.

Otozamites Braun, 1842.

Otozamites sp.

Type: CU 421.01 Cl.

Collection: J.D.Lovis and I.L.Daniel, West Quail Flat, Feb.1988.

Plate 14C.

Description: leaf pinnate, fragment 30 mm. long, 25 mm. wide, with six pinnae attached to upper side of rachis, rachis not completely overlapped by pinna bases, pinnae on same side overlapping. Substance of leaf moderately thick.

Pinnae alternate, nearly circular with asymmetric base, increasing in size *apically* 8 - 16 mm. long, 10 - 12 mm. wide, with long axis at an angle of 60^0 to rachis; region of attachment contracted, about a quarter of basal margin, near basiscopic angle; acroscopic angle slightly overlapping rachis, rounded, slightly expanded but scarcely forming an auricle; basiscopic angle scarcely expanded; margins of pinna entire, not distinctly thickened or reflexed.

Veins broad, radiating from point of attachment, forking to attain a concentration of about 8 per cm. at widest part of pinna, ending in apical margin.

Cuticle unknown.

Discussion: only one specimen has so far been found. It appears to be the basal part of the leaf since the size of the pinnae increases *apically*. A single pinna found in the same block has similar venation but is of distinctly ovate form, and lacks an apex. While it may represent the pinna form from the middle of the leaf, this cannot be known until further specimens are found. Therefore it is not included in the description.

Comparison: the generic determination follows from the "Key to the Yorkshire genera of leaves" of Harris (1969, p.3). Using his (loc.cit. p.11) "Field Key to the Yorkshire species of *Otozamites* based on the middle region of a typical leaf" the present fossil keys out to *O.marginatus* (Saporta). That species is represented by two specimens from Yorkshire, both of which agree with the holotype figured by Saporta (1875) in having a clearly sharply reflexed margin. Also, its veins are obscure ridges at a concentration of about 50 per cm. These two characters alone are sufficient to exclude the present fossil from *O.marginatus*.

Harris (loc.cit. p.55) notes that "*O.marginatus* resembles exceptionally small leaves of *O.beani* in the size and shape of the pinnae, and also the normal leaves of *O.tenuatus*". The pinnae of the present fossil are much smaller, more rounded and with fewer veins than those of *O.beani*, although the solitary pinna not included (see discussion above) approaches its shape.

The leaf of the present fossil is much broader than that of *O.tenuatus* (2.5 cm. c.f. 0.6-0.8 cm.), the pinnae are set at a wider angle (60° c.f. 45°), and they do not completely overlap the rachis, but in many other characters there is some agreement, especially the vein density (8 per cm. c.f. 5-7 per cm.). However Harris (loc.cit p.52) states "*O.tenuatus* is only reliably determinable when its cuticle is available. Its form is indistinguishable from the Italian *O.bunburyanus* Zigno 1881 (at least on present knowledge)".

Of the bennettite species described by Douglas (1969) from the Cretaceous of Victoria, the only species to which the present fossil shows some similarity is *Ptilophyllum boolensis*. Originally placed in *Otozamites* (Douglas, 1963), this species was transferred to *Ptilophyllum* (Douglas, 1969) because of the presence of sunken subsidiary cells bearing overhanging papillae. It has very small (2-4 mm. long, 1-2 mm. wide) oval pinnae set at a wide (70° - 90°) angle to the rachis, and has a distinctive cuticle.

Ptilophyllum Morris, 1840, p.327, expl.pl.21.

Ptilophyllum seymouricum McQueen sp. emend.

1956 *P.seymouricum* McQueen, p.685, Text-fig.3, Figs.8,9.

Holotype: B356/30, Seymour Stream (N.Z.G.S. Coll.).

Figured paratype B.356/4, Seymour Stream (N.Z.G.S. Coll.).

Collection: E. Bank, Seymour Stream, 2 chains upstream from Coal Creek, R.A.Couper and R.P.Suggate, 1953.

Other material included: Alexander McKay Flat, 212.08 - 11, 212.16; East Quail Flat, 310.09 (cuticle only, S.E.M. stub 6); *Ptilophyllum* Ridge, 522.24 (S.E.M. stubs 76, 89), 522.28 (bold-type measurements below), 522.42 (S.E.M. stub 75) plus 24 other specimens.

Plates 17-19.

Emended and Amplified Description: leaf pinnate, linear to narrowly elliptic, length (incomplete) up to 18 cm., 3 cm at widest, tapering gradually below and rather more quickly above to 1 cm., apex acute, with single apical pinna, ^{A laminate region} base acute, rachis 0.1 cm, slender, smooth, straight, petiole short, stout, 1-2 cm. long, 0.2 cm. wide.

Pinnae alternate, 4 per cm, falcate or straight then curving forward, apex acute, ^{towards leaf apex} upturned, those in middle of leaf at about 65^0 to rachis (60^0 near base 45^0 near apex), separated by gaps of 0.0-0.02 cm., length of medial pinnae about 1.8 cm., of apical and basal pinnae 0.5 cm., width of medial pinnae 0.2 cm., of apical and basal pinnae 0.15 cm., i.e. width of pinna about one-ninth its length. Pinnae attached to upper surface of rachis apparently by the whole of the base, ^{acroscopic} basal angle rounded, ^{acroscopic} margin concave, ^{basiscopie} basal angle slightly decurrent or acutely rounded, ^{basiscopie} margin convex.

Substance of lamina of medium thickness often concealing veins, upper surface smooth, veins

arising from whole base of pinna at the same angle as pinna axis and running parallel to lateral margins then converging to apex, rather seldom branched away from rachis, 20 per cm. in middle of pinna, 4 per pinna.

Cuticle moderately thick, hypostomatic. Adaxial cuticle thinner, more fragile than abaxial, without stomata or trichomes, showing longitudinal files of uniform rectangular cells; anticlinal flanges distinct, narrow, only longitudinal flanges slightly sinuous, surface of cell flat, without papillae, veins not marked by differentiation of cell shape. Abaxial cuticle showing stomata in bands between veins, stomatal bands about twice the width of vein bands, epidermal cells in longitudinal files, uniform, rectangular, only longitudinal anticlinal flanges slightly sinuous, about as much as adaxial flanges, surface of cell flat, without papillae, apparently occasional trichomes with multicellular bases.

Stomata scattered or in three to five short longitudinal rows within bands, seldom occurring close to one another, nearly all oriented transversely, occasionally obliquely, aperture about 25 - 35 μm . Subsidiary cells small, surface rather thickened, sometimes each bearing a short papilla projecting partly over surface of guard cell, papilla not expanding from its base, apex rounded, wall thickly cutinised but interior hollow. Guard cells sunken, flanges between guard and subsidiary cells semicircular, thickened, extending under subsidiary cells, inner stomatal ledge of guard cell very thick, crescent-shaped, about 40 μm . long, extending inwards.

Discussion: no further collections have been found at the Seymour Stream locality of McQueen (1956). However, very similar leaves have been found at two other sites in the study area. Almost complete leaves are found at *Ptilophyllum* Ridge in a cross-bedded red sandstone interpreted as deposits in a small, probably shallow, seasonally dry lake. Short segments of leaf are found at Alexander McKay Terrace in massive grey sandstone interpreted as crevasse splays. In both sites they are fossilised with dicotyledonous and various other leaf types which are essentially undamaged. It is therefore suggested that *Ptilophyllum* is a rather delicate leaf with an easily broken rachis.

McQueen (1956,p.685) states that *P.seymouricum* "is distinguished by the wide spacing of the pinnae, which are their own width apart as if forced apart by the insertion of the alternate pinnae on the rachis". This description was confirmed by re-examination of the holotype, but none of the present collection exhibit this feature, the greatest separation of pinnae being one tenth the width of a pinna. However, the dimensions of *P.seymouricum* for all other characters fall within the ranges for the present

collection. It is therefore accepted that the *Ptilophyllum* Ridge and Alexander McKay Terrace collections are conspecific with *P.seymouricum*, and that only one species of *Ptilophyllum* is present in the middle Clarence valley. However, in view of the atypical spacing of pinnae of the holotype, the range of dimensions of the present collection, and the preparation of cuticle from it, it is thought desirable to emend and amplify the description of the taxon.

Comparison: *P.acutifolium* Morris ex Arber of the N.Z. Jurassic has triangular pinnae (1-4 cm in length and 0.3 cm across at the base) which are straight or, more usually, falcate, with 5 veins per pinna, the veins usually dividing once.

Of ten *Ptilophyllum* species described by Douglas (1969) from the Early Cretaceous of Victoria, Australia, only *P.fasciatum* shows any similarity, but its pinnae are shorter (0.5-1.0 cm.) and wider (0.2-0.3cm.) and may be at a greater angle (60^0 - 90^0) than in the Clarence species. Also, its pinnae have more veins (5-8) which diverge and branch once or twice at very acute angles. All the others, e.g. *P.boolensis*, are of a different order of size being much smaller leaves with shorter pinnae.

Of the three species of *Ptilophyllum* described by Harris (1969) from the Jurassic of Yorkshire, only *P.pectinoides* shows similarity of dimensions to *P.seymouricum*. However the pinnae of *P.pectinoides* are usually straight. The dimensions of these two species and of two unusual specimens from Yorkshire are compared in Table 6.1. The greatest difference however lies in the epidermis as shown by cuticular characters. The present species has stomata which lack large papillae or are non-papillate, are arranged in bands greater in width than the vein bands, and have anticlinal walls which are only slightly sinuous. This contrasts with *P.pectinoides* where large papillae project over the guard cells and usually contact opposite papillae, stomatal bands are about equal to the vein bands in width, and all the anticlinal walls are very sinuous. These differences may reflect ecological differences, especially climate, the *P.pectinoides* epidermis apparently being adapted to xeric conditions.

6.4. Key to Clarence Pinnate Cycadales and Bennettitales

- 1(a) Pinnae placement regular, crowded. 2
- (b) Pinnae placement irregular, not crowded. 3
- 2(a) Pinnae circular. *Otozamites* sp.
- (b) Pinnae falcate, ~~or straight, long, narrow.~~ *Ptilophyllum seymouricum*
- 3(a) Pinnae set approximately 90^0 to rachis. 4
- (b) Pinnae set at less than 90^0 to rachis. 7
- 4(a) Pinna length/width ratio approximately 1:1. 5
- (b) Pinna length/width ratio not 1:1. 6
- 5(a) Pinnae regular, triangular, secondary veins do not curve
round indentation, upper margin not at 90^0 to rachis.
Anomozamites blechnoides
- (b) Pinnae irregular, roughly triangular, secondary veins
curve round indentation, upper margin at 90^0 to rachis.
Basal *Nilssonia pseudocompta*
- 6(a) Pinnation irregular, gap between pinnae < pinna width;
length/width ratio 1.3:1 - 3:1; pinnae rhomboid,
apex truncate or obtusely rounded.
Pterophyllum sp.C
- (b) Pinnation regular, gap between pinnae = pinna width;
length/width ratio 10:1 - 5:1; pinnae elongate tapering,
apex acutely rounded.
Pterophyllum rectipinnatum

- 7(a) Pinnae approximately 80^0 to rachis; indentation rounded, often not to rachis, apex truncate, secondary veins obscure, approx.20/cm.

Apical Nilssonia pseudocompta

- (b) Pinnae approximately 45^0 - 65^0 to rachis, indentation sharply acute to rachis, apex truncate, secondary veins perceptible but not clear, 24/cm.

Pterophyllum sp.A

- (c) Pinnae approximately 45^0 to rachis; indentation rectangular, asymmetrical, to rachis; secondary veins obvious and clear, 10/cm.

Pterophyllum sp.B

6.5. Conclusions

The records of fossil cycadophytes in New Zealand (see Appendix 2.2) suggest that in Jurassic times only three pinnate species of cycadophyte existed, namely *Nilssonia compta* (Phillips) Schenk, assumed to belong in the Cycadales, and *Ptilophyllum acutifolium* Morris and *Pterophyllum matauriensis* Hector ex Arber, assumed to belong in the Bennettitales. All were described in Arber (1917).

At least eight species of pinnate cycadophytes are now known from the Cretaceous of New Zealand. Of these, one (*N.pseudocompta*) belongs in the Cycadales. The remainder belong in the Bennettitales, two (*P.seymouricum* and *Otozamites* sp.) with pinnae attached to the top of the rachis, and the remaining five with pinnae attached to the side of the rachis. This fundamental difference in bennettite leaf structure is correlated with different reproductive structures (Harris, 1969) which suggests they belonged to distinct genetic lines.

Thus, during Jurassic and Cretaceous times, leaves attributed to the Cycadales remained relatively unchanged and undiversified. Meanwhile, leaves attributed to the Bennettitales, but more particularly the form genus *Pterophyllum* (which could also include *Anomozamites blechnoides*), appear to have undergone considerable morphological diversification. Although the genus *Pterophyllum* is "likely to be somewhat heterogeneous" (Harris, 1969, p.92), the diversity of its leaf form in the N.Z. Cretaceous suggests that, at least in S.E.Gondwana, there was diversification of reproductive species from the single known Jurassic species, *P.matauriensis*.

7.1. Introduction

Although McKay (1886, p.101-102) gave a detailed account of the rocks and plant fossils occurring at the "southern end of Quail Flat" (now known as East Quail Flat) which included "fine splintery black shales crowded with long slender leaves having parallel venation" (described in Chapter 8 as *Agathis clarencianum*), he apparently failed to observe an abundance of small, cuneiform leaves with dichotomising veins (described below as *Ginkgo cuneiformis* sp. nov.) which occur in very similar strata close by. Indeed, the wide distribution of these fossils in the study area makes his failure to record this leaf type puzzling.

Equally puzzling is the identity of one of the fossils to which he is referring when he describes (loc.cit. p.99-100) two of the "fern" species collected at Red Hill Stream as "remarkable as not common to beds of this age in New Zealand, and as indicating a Jurassic rather than a Cretaceous age". The first, "Taeniopteris" is probably *Taeniopteris stipulata*. Of the second he writes "the other plant has certainly not been before obtained from New Zealand strata, and closely resembles *Danaeopsis* and *Sphenophyllum* [sic] of the Triassic and Jurassic of India". From the perspective of the present day, without knowing on what source McKay was relying, it is very difficult to visualise how any fossil can resemble both *Danaeopsis* and *Sphenophyllum*, but it is possible his "Sphenophyllum" may refer to the leaves described here as *G.cuneiformis*.

Several previous authors have attributed New Zealand fossils of various ages to the Ginkgoales. Details are presented in Appendix 2.3.

7.2 SYSTEMATICS

Order Ginkgoales

Genus *Ginkgo*

Ginkgo cuneiformis sp.nov.

Holotype: CU 300.20 Cl

Collection: J.D.Lovis et al., Dec. 1978.

Diagnosis: leaf simple, cuneate, bilobed but not deeply dissected by sinus, two veins emerging from base and bifurcating at varying distance along lamina, scarcely petiolate.

Other material included: Horse Flat, 111.01-3, 120.05, 121.07; Alexander McKay Terrace, 215.02-05, 217.18, 220.14; East Quail Flat, 300.01-42 (many specimens), 310.18, 311.01^{*}, 322.06^{*}, 322.09^{*}, 330.02, 330.41; West Quail Flat, 410.22; Ptilophyllum Ridge, 522.63; Lower Seymour Stream, 613.10, 614.02; Upper Seymour Stream, 718.54^{*}. (Specimens marked ^{*} were used for cuticle investigation).

Plate 20A-F, 21A-C.

Derivation: from *cuneiformis* - Latin meaning wedge-shaped, referring to the lamina form.

Description: leaf simple, cuneate, usually straight-sided but occasionally curved, 2.5 to 4.3 cm. long, 1.0 to 2.9 cm. at widest gradually narrowing to 0.1 to 0.2 cm at base, usually bilobed, occasionally apparently with complete apical margin, sometimes lobed unequally or with successive subordinate lobes. Apical sinus up to 0.5 cm. deep, with a rounded base, lobe apices rounded. Lamina coriaceous, sometimes resinously translucent, and occasionally with scattered resin bodies. Leaf scarcely petiolate, the edges of the proximal part sometimes being slightly folded but not rolled, with its base broadened.

Veins obvious, subparallel, bifurcating at varying distance along lamina, remaining parallel to the lateral margin, terminating in the distal margin. Two veins at the lamina base, and approximately 17 per cm. at the level of the sinus base.

Cuticle unequally amphistomatic. Abaxial cuticle approximately equal in thickness to the adaxial but more fragile. Cells on both surfaces differentiated into vein and interveinal areas, but those of the adaxial cuticle more distinctly differentiated than those of the abaxial cuticle. Anticlinal flanges between epidermal cells of medium thickness and usually straight, but those of the adaxial cuticle occasionally slightly sinuous.

Adaxial cuticle (Plates 20E,21A):

Epidermal cells of vein areas linear-elongate often with oblique end walls, in files in bands 5 to 15 cells wide, mostly oriented parallel to long axis of leaf, with occasional pairs or short files of cells oriented transversely, lacking papillae, but a few with hairs up to 170 μm long; anticlinal flanges usually straight, but longitudinal flanges occasionally slightly sinuous with wavelength 3 μm and amplitude 2 μm . Twentythree cells measured along two adjacent files (Files 1 & 2, Plate 21A, and Table 7.1) are 40 to 100 (mean 64) μm long, and 20 to 35 (mean 27) μm wide.

Epidermal cells of interveinal areas irregularly polygonal, lacking papillae or hairs, in irregular files. Twentythree cells measured along two adjacent files (Files 3 & 4, Plate 21A, and Table 7.1) are 25 to 72 (mean 50) μm long, and 15 to 40 (mean 28) μm wide. A t-test of the length/width ratios of cells of vein and interveinal areas show them to be significantly different ($0.2 < p < 0.5$).

Stomata scattered or in short irregular rows in narrow bands, randomly oriented, and less frequent than on the abaxial surface, with a density of 30 per cm^2 , Stomatal Index of interveinal band = 14.8.

Abaxial cuticle (Plates 20B-D & F,21B&C):

Epidermal cells of vein areas mostly linear elongate often with very oblique, overlapping end walls lacking papillae or hairs, in irregular files in irregular bands three to four cells wide; anticlinal flanges straight. Twentyfive cells measured along two adjacent files (Files 1 & 2, Plate 21B, and Table 7.1) are 50 to 112 (mean 70) μm long, and 15 to 31 (mean 25) μm wide.

Epidermal cells of interveinal areas linear elongate, rectangular or irregularly polygonal, lacking papillae or hairs, in very irregular files. Twentyfive cells measured along three adjacent files (Files 3,4 & 5, Plate

21B and Table 7.1) are 37 to 87 (mean 60) μm long, and 19 to 34 (mean 26) μm wide. A t-test of the length/width ratios of cells of vein and interveinal areas show^s them not to be significantly different. Stomata scattered in wide bands and randomly oriented at a density of 40 per mm^2 . Stomatal Index = 16.8.

Stomatal apparatus (Plate 20C&D^F) slightly raised, aperture circular when open, up to 19 μm long, with four, five or six subsidiary cells, some being divided tangentially (Plate 20D) to make the apparatus partially dicyclic. Subsidiary cells lack thickening or papillae. Intercellular flanges between subsidiary cells thin and steep. Guard cells sunken below the level of the epidermis, up to 30 μm long and 30 μm across when open. Flanges between guard cells and subsidiary cells large and circular, coming to a point towards poles, partly covering subsidiary cells except at poles. Inner stomatal ledge of medium thickness, projecting inwards, but not extending beyond stomatal flange at poles.

Discussion: comparison of stomatal apparatus structure and distribution on the abaxial cuticle of *Ginkgo cuneiformis* with those of *G. biloba* (Plates 20-22) suggest the former is correctly placed in the genus *Ginkgo*. However, the presence of stomata on the adaxial cuticle, together with leaf form differences (discussed in Sections 7.3 and 7.4) indicate *G. cuneiformis* is a new species. The leaves occur in large numbers as closely overlapping "leaf beds" in locally derived sediments. They are randomly oriented on the bedding planes, and occur in numerous horizons within any particular lithologic unit. The expanded leaf base is not a pulvinus. This suggests the leaves were derived from a locally abundant plant which was seasonally deciduous.

During maceration of fresh *Ginkgo biloba* leaf samples, large bubbles forced the separation of adaxial and abaxial cuticles. The veins all held to the abaxial cuticle when the leaf was mechanically split. During maceration of samples 322.06 (bulk maceration 59) and 322.09 (bulk maceration 58), the fossil cuticles similarly were forced apart by bubbles (Plate 20F). One cuticle, assumed to be the adaxial, held together better and was cleaner, or more easily cleaned (e.g. with a gentle water jet) than the other. It curled more in Schultze's solution, but then unrolled in alcohol. The other cuticle, assumed to be the abaxial, was more fragile and retained mesophyllous material (which was difficult to remove) with veins showing clearly as dark lines.

7.3. Comparison With Other Fossil Species.

Of five species of *Ginkgo* described by Harris (in Harris, Millington and Miller, 1974) from the Jurassic of Yorkshire, only *G.huttoni* (Sternberg) Heer emend. Harris has a leaf of similar size to *G.cuneiformis*. However, it differs in having a distinct petiole and stomata only on the abaxial surface. Only one of the five, *G.whitbiensis*, is amphistomatic. It is a small leaf which is clearly petiolate and has a deep sinus dividing the lamina into two lobes, each of which is usually divided by a sinus only slightly less deep.

Douglas (1961, 1965, 1969, 1970), under the order Ginkgoales and the genus *Ginkgoites* Seward, described six species from the Cretaceous of Victoria, Australia. Three, *G.australis*, *G.multiloba* and *G.waarrensis*, are described with cuticle. *G.waarrensis* is known only from a single fragment and is typified by its cuticle. The other three species, *G.sp."*a", *G.sp."*b" and "ginkgoalean leaf type a", lack cuticle but have distinctive lobation and venation.

Comparison of the cuticular characters of *Ginkgo cuneiformis* with those of *Ginkgo biloba* and some other fossil species (Table 7.2) shows that it is distinctive. The most significant difference is that *G.cuneiformis* is the only one with an appreciable number of stomata on the adaxial surface. Only *G.whitbiensis* approaches this condition. The lack of papillae and/or many hairs on epidermal cells of *G.cuneiformis* is a character shared with *G.whitbiensis*, *G.waarrensis* and *G.biloba*, as is the moderate density of stomata on the abaxial surface. Furthermore, *G.cuneiformis* and *G.biloba* are the only species which lack papillae on, and/or thickening of, subsidiary cells. However *G.waarrensis* and *G.biloba* both have sinuous anticlinal flanges. Thus *G.cuneiformis* and *G.whitbiensis* have the most characters in common. Indeed the only marked difference between their cuticles is the reduced number of adaxial stomata and the presence of papillae on, and thickening of, the subsidiary cells of the latter. It is because of this similarity of cuticle that I follow Harris in assigning the present fossil to the genus *Ginkgo*.

While the presence or absence of papillae has been considered of taxonomic importance (e.g. Douglas, 1970, p.32), it is a character which may well be influenced more by phenotypic (plastic) than genotypic factors, and I hesitate to suggest relationship on such grounds. Furthermore, at least for the species considered here, the number of stomata on the adaxial surface decreases with increasing

modification of subsidiary and epidermal cells, again suggesting a phenotypic basis for the differences. However, it should be noted that in fossil material it is impossible to distinguish genetic from purely plastic, environmentally induced differences. In view of the lack of reproductive organs, one must accept the obvious differences between the fossil taxa and describe them as form species.

7.4. Comparison of *Ginkgo*/*Ginkgoites* Fossil Leaf Forms with *G.biloba*

Sporne (1974, p.165) states "The leaves of *Baiera*, *Ginkgoidium* and *Ginkgoites* were like those of modern *Ginkgo* in having a distinct petiole". He describes (loc.cit. p.167) the leaves of *Ginkgo biloba* as "fan-shaped, with beautifully regular dichotomous venation, and have a petiole which receives two endarch vascular strands. Those on the long shoots are mostly bilobed, but those on the short are entire". He continues "Until recently it has always been stated that the leaves are hypostomatic. However, Kanis and Karstens [1963] have recently shown that this is not entirely true, since the leaves from long shoots (of male trees in particular) tend to have a few stomata in the upper epidermis. The stomata in the lower epidermis occur in broad bands between the veins and are surrounded by four, five or six accessory [here termed subsidiary] cells with finger-like processes projecting over the guard-cells".

Hara (1980) has described the early ontogeny of the leaves of long shoots of *Ginkgo biloba*. He showed that the lamina of the leaf is derived from a protuberance on the adaxial side of a leaf buttress. The first bifurcation of this protuberance occurs vertically in the plane of the stem and serves to form the major sinus which establishes the bilobation of the mature leaf. The second bifurcation occurs vertically at right angles to the first, i.e. tangential to the stem. It is succeeded by bifurcations between the first and second bifurcations, and between the second bifurcation and the edge of the protuberance. Thus, the abaxial surface of the lamina is derived from the outer surface of the protuberance and the adaxial from the depressed inner surface formed by the first and second bifurcations.

It would seem from the lamina shape of *G.cuneiformis* that in this fossil species the first bifurcation usually occurred, but that the second occurred only rarely and somewhat randomly. In contrast, *G.waarrensis* and *G.whitbiensis* show well defined first and second bifurcations, while the more

dissected leaves of other *Ginkgo/Ginkgoites* species show the presence of subsequent bifurcations as well.

Hara (1980, p.1) "supposed that thick veins along both edges of the lamina are differentiated by an uneven dichotomous branching system of procambia caused by positional relationships: both edges of the lamina are derived from the parts of the protuberance just above a pair of procambia which come from the stem". Each edge spirals inwards towards the second bifurcation and retains the thick veins close to the margin (loc.cit.Figs.11,12 and p.10-11). The presence of just two veins in the proximal part of *G.cuneiformis* apparently corresponds to these procambia, and to the two adaxial veins traversing the petiole of *G.biloba*. However, the latter also has a number of abaxial veins, apparently of smaller dimensions, arranged in an arc around the adaxial veins. All traverse the petiole before dichotomising.

7.5. Petiole Development

Hara (1980, p.8) commented that "the growth of a primordial petiole is prominent in older leaves" of axillary buds growing in spring "but it is not prominent in winter buds". It is suggested here that the constriction apparent in developing buttresses (loc.cit. Fig.6) results from reduction in the rate of lateral extension of the proximal portion of the buttress compared to the rate of lateral extension of the distal portion, rather than the "growth" of a petiole. Examination of a mature *G.biloba* "petiole" shows that it is produced by inrolling towards the adaxial surface of the blade margins in the proximal part, while a more expanded lamina in the distal part is achieved only by continued dichotomy of the veins. It should be noted that in *G.biloba* the positions of dichotomy of the veins across the lamina is not as consistently regular as suggested by Sporne (see reference above) or Hara (1980, Fig. 19). The individual branches of one dichotomy do not always undergo their subsequent dichotomy at the same distance from the initial dichotomy. This feature is also particularly evident in *G.cuneiformis*.

Kaplan (1973) suggested the monocot leaf is of two parts, a distal unifacial upper section and a proximal bifacial sheath. Where the monocot leaf is more sharply articulated, the proximal section differentiates into lamina and "petiole" (and sheathing base) while the distal section remains rudimentary ("Vorlauferspitze"). He has shown, on the other hand, that in the dicotyledon leaf the petiole is

developed from intercalary meristem between an upper (blade) zone and a lower (base) zone, either or both of which may be expanded. The lack of differentiation of the *Ginkgo* leaf (and presumably of *Ginkgoites*) suggests it is not able to be subdivided into sections, and must be regarded as a single entity.

Isebrands and Larsen (1980, p.24, Table 1) showed that in the ontogeny of *Populus deltoides* leaves, the apical three of the eight secondary veins begin differentiation before development of the petiole commences. This suggests that the petiole of dicotyledons develops subsequent to, and independent of, the lateral expansion of the lamina. The terete, manouverable petiole is unique to dicotyledons but is absent in some, e.g. *Dracophyllum*. Thus, in terms of Kaplan's intercalated petiole, *Ginkgo* (and presumably *Ginkgoites*) does not have a true petiole. It would be better termed a "pseudopetiole".

The observation that *G.cuneiformis* from the "coastal" Clarence deposits lacks a distinct pseudopetiole and has few vein dichotomies to produce a rather narrow, wedge-shaped leaf, while *G.australis* and *G.multiloba* from the approximately coeval "continental" Victorian sediments, have distinct pseudopetioles and many vein dichotomies to produce broad, fan-shaped leaves, suggests the degree of "petiolation" is environmentally influenced. On the other hand, the serial development of these structural features, in terms of Hara's work, exhibited by *G.cuneiformis*, *G.waarrensis* and *G.whitbiensis*, together with the variations in lobation discussed above, suggests an evolutionary development from an apetiolate, narrow leaf with a retuse apex, to a petiolate, broad, much segmented leaf, with *G.cuneiformis*, in spite of its Cretaceous age, representing the most primitive morphotype. This is the reverse of the "evolutionary development towards reduction in lamina segmentation" proposed by Douglas (1970, p.32) on stratigraphic evidence.

CHAPTER 8. *AGATHIS* LEAVES

8.1. INTRODUCTION

McKay (1886, p.102) recorded the presence of "*Dammara* [= *Agathis*] leaves" at the "southern end of Quail Flat" (now known as East Quail Flat). More recently, among the fossils collected by J.D.Lovis from Seymour Stream in 1978 is a foliage-bearing shoot with spiral phyllotaxis, which was recognised by the late Tom Harris as *Agathis*. This specimen was initially recognised as being distinct from any previously described New Zealand fossil species by means of macromorphological characters alone. It was among the first in the present study to have cuticle extracted for light microscope and S.E.M. studies. Its araucariacean affinities were immediately apparent and to determine its relationship to modern Araucariaceae, leaf cuticular micromorphological characters were analysed using numerical taxonomic procedures (Sections 3.3 and 8.3). The only previous use of cuticular characters for the determination of a New Zealand araucariacean was by Bose (1975) who employed them to establish that *Araucaria haastii* Ett. from the Upper Cretaceous at Shag Point is correctly placed in *Araucaria*.

The cuticular micromorphological characters of the fossil are compared with those of some extant species of *Agathis* and of *Araucaria* sect. *Columbea* by cluster analysis of association coefficients for 35 characters which indicates the empirical affinities of individual taxa. This suggests the fossil is most similar to, but distinct from *Agathis australis* (the extant N.Z. endemic species, "kauri"). It is described below as *Agathis seymouricum* sp.nov. These two taxa are shown to be closely allied to the New Caledonian and Queensland species investigated.

Stepwise discriminant analysis is used to indicate the characters which best discriminate between *a priori* groups derived from the cluster analysis and from the taxonomic schemes of Whitmore (1980) and Page (1980). It is also used to test statistically the ability of the cuticular character set to reproduce taxonomic systems established on other totally unrelated characters of different structures. The cuticular characters reproduce the taxonomic scheme of Whitmore.

In describing Tertiary Araucariaceae from southeastern Australia, Cookson and Duigan (1951) grouped a) fossil and extant *Araucaria* species on the basis of six types of stomatal distribution and b) fossil and extant *Agathis* species on two types of stomatal orientation.

To compare *A.seymouricum* with the Australian fossil species *Agathis yallournensis* Cookson & Duigan and *Agathis parwanensis* C. & D., a data set of 13 of the characters previously used for comparison of the Clarence fossil with extant taxa was prepared from the descriptions of Cookson and Duigan (1951). The data which they gave for *A.australis* together with my own data for *A.australis* were included. Cluster analysis suggests that *A.seymouricum* and *A.australis*-(my data) are more similar to each other than they are to the Australian fossils and *A.australis*-(Cookson & Duigan data). Details are discussed in Section 8.5.3.

Subsequent to these comparative studies of *A.seymouricum*, a fossil originally thought to have ginkgoalean affinities was found to have cuticular micromorphology typical of *Agathis*. It is described below as *Agathis clarencianum* sp.nov. and is almost certainly the fossil to which McKay (1886, p.99) was referring when he recorded an "abundance of a long narrow leaf with parallel venation" from Red Hill Creek. He also observed (loc.cit. p.102) that, at East Quail Flat, "fine splintery black shales are crowded with long slender leaves having parallel venation". The Red Hill site is now obscured and unworkable, but the East Quail Flat material has been relocated and recollected.

A set of 32 characters similar to those used for comparison of *A.seymouricum* with extant taxa is used to compare this second species with *A.australis*, *A.seymouricum*, *A.yallournensis* and *A.parwanensis*. Cluster analysis of these data suggests that *A.clarencianum* is more similar to the Australian fossils than to *A.seymouricum* or *A.australis*. Inclusion of the extant Australian *Agathis robusta* fails to disrupt this clustering, suggesting that *A.seymouricum* rather than *A.clarencianum* is the most likely ancestor of *A.australis*. Details are discussed in Section 8.5.

8.2 TAXONOMY OF the genus *AGATHIS*

Whitmore (1980) has performed a valuable service in producing some order out of the chaos of *Agathis* taxonomy. His reduction of the number of species recognised to thirteen is based on male cone morphology since "with only a few exceptions, variation in leaf size and shape exhibits no disjunctions but is as great within as between species" (loc.cit.p.43). These taxa also, for the most part, possess distinct geographical distributions. Relying principally on microsporophyll characteristics, he in effect subdivides the genus into five informal groups: 'group B' comprising eight spp. (*A.australis* of N.Z.; *A.corbassonii*,

A.lanceolata and *A.montana* all of New Caledonia; *A.macrophylla* of Melanesia; *A.atropurpurea* of Queensland; *A.dammara* and *A.borneensis* of Malesia), 'group A' comprising two species (*A.microstachya* of Queensland and *A.labillardieri* of New Guinea), and three monospecific entities, namely *A.moorei* and *A.ovata*, both of New Caledonia, and *A.robusta* of Queensland and New Guinea. To date no male araucariacean reproductive structures have been found in the middle Clarence valley. Thus, relating *Agathis seymouricum* and *A.clarencianum* to the taxonomy of Whitmore cannot be achieved by direct comparison.

Page (1980) surveyed the external micromorphological surface structure of leaves of living species of the genus *Agathis* from throughout its range using the S.E.M. for photographing samples. He divided the genus into three distinct "leaf groups" on the basis of four characters and related these leaf groups to the geographic distribution of the genus. One group contains only *A.australis*. The remaining two groups do not correlate with Whitmore's grouping, a circumstance which led them jointly to declare (Whitmore & Page 1980, p.408) "that *Agathis* is a genus of closely related species with only subtle differences between them and not forming marked subgeneric groups".

Stockey and Taylor (1981) reviewed the micromorphology of leaf cuticle as revealed by the S.E.M. of four species of *Agathis* using characters observed mainly on the inner surface of the abaxial cuticle. They related the *Agathis* species they studied to the divisions of Cookson and Duigan (1951) but suggested characters in addition to stomatal orientation which would prove taxonomically useful.

The generally poor preservation of the leaf cuticle of *Agathis seymouricum* precluded the use of some of the characters of Page and of Stockey and Taylor. Also the number of characters and taxa investigated by the latter authors were insufficient for application of satisfactory numerical taxonomic analysis. Therefore in the present study a mostly different set of characters which were present in the fossil was investigated.

The taxonomic position of *Agathis seymouricum* relative to extant taxa was determined by comparison with twelve *Agathis* and two *Araucaria* sect. *Columbea* specimens. Herbarium samples were macerated using the same procedure as for preparation of the fossils. The taxa investigated were *Araucaria araucana* (Molina) K.Koch, *A.angustifolia* (Bertolini) O.Kuntze, *Agathis australis* (D.Don) Lindley ex Loudon (following Franco 1949) or (Lambert) Steudel (following Whitmore 1980), *A.brownii* (hort.ex Lemaire) L.H.Bailey, *A.lanceolata* Lindley ex Warburg, *A.macrophylla* (Lindley) Masters,

A.obtusa (Lindley) Masters, *A.ovata* (C. Moore ex Vieillard) Warburg, *A.palmerstonii* (F.Mueller) F.M.Bailey, *A.robusta* (C.Moore ex F.Mueller) F.M.Bailey, *A.vitiensis* (Seeman) Benthams & Hooker f. (two specimens from different localities of Fiji) and two previously unidentified specimens of *Agathis* from New Caledonia. Of these, three taxa are reduced to synonymy in Whitmore's revision:- *A.obtusa* and *A.vitiensis* = *A. macrophylla*, *A.palmerstonii* = *A.robusta*. A fourth taxon, *A.brownii*, is treated as *species dubia*. The names cited are those to which the respective collections are attributed in the CANU and CHR herbaria, and are retained for the presentation of results. Their source and, where applicable, their synonymy in Whitmore's revision are presented in Appendix 3.

8.3. NUMERICAL TAXONOMIC ANALYSIS OF CUTICULAR CHARACTERS OF

Agathis seymouricum

Comparison of the cuticular micromorphology of *A.seymouricum* with that of 14 extant taxa (Table 8.1) was carried out by cluster analysis of association coefficients for 35 characters using the Mint 6 computer programme (Rohlf 1971) and by stepwise discriminant analysis using the BMDP7M computer programme (Dixon 1981)(see Section 3.3 for details).

The characters employed, their correlation, and those used by previous authors are given in Table 8.2. Character states data are given in Appendix 3. Characters were chosen on the basis of the possibility of measuring them in the fossil and mostly follow those of Dilcher (1974). Measurements were made directly from the S.E.M. photographs. None of the highly significant correlations of characters are "logical" so no character need be removed.

8.3.1. Association Coefficient Grouping

The phenogram established by cluster analysis of association coefficients of all 15 OTUs listed in Table 8.1 shows clear distinction between *Araucaria* sect. *Columbea* (OTUs 1, 2) and *Agathis* (OTUs 3-15) (Fig 8.1a).

Within *Agathis*, certain groups of taxa are clearly equivalent to the species upheld by Whitmore, especially *A.australis* with *A.seymouricum* ("Australis" group), *A.brownii* and *A.palmerstonii* with *A.robusta* ("robusta" group), *A.vitiensis* "F" with *A.macrophylla* ("macrophylla" group) and *A.sp.*"Mt. Mou" with *A.vitiensis* "N" ("vitiensis" group). The group including *A.lanceolata*, *A.sp.*"R. Bleue", *A.obtusa* and *A.ovata* (OTUs 5, 7, 9, 10 respectively) is not clearly divided. It would be expected under Whitmore's scheme that OTUs 5 and 7 would form a group, OTU 9 would link with "macrophylla" and OTU 10 would stand alone. Furthermore this group is closely linked to the "robusta" group (OTUs 4, 11, 12).

When *A.seymouricum* is removed from the computation (Fig.8.1.b) the forced association of *A.australis* with *Agathis* species from outside New Zealand disrupts all but the "Araucaria" group, the "macrophylla" group and the "vitiensis" group. Further reduction to 9 OTUs (Fig.8.1.c) to attempt to resolve the "robusta", "lanceolata" and "ovata" groups again retains only the "macrophylla" and "vitiensis" groups as distinct entities.

8.3.2. Discriminant Analysis Grouping

Testing of the ability of the cuticular characters to reproduce taxonomic schemes using the BMDP7M programme was conducted under three broad categories: association coefficient groups, Whitmore species groups, and Page leaf groups. The different *a priori* grouping of OTUs within each category is given in Table 8.3 together with the particular characters selected by BMDP7M as significantly discriminating between *a priori* groups.

It should be noted that this confirmation of groups is in the nature of a self-fulfilling prophecy and only serves to identify the characters most responsible for the grouping. However, stepwise discriminant analysis can also be employed to test the capacity of one character set to reproduce a

taxonomic classification based on other, totally unrelated characters. In this case the character set employed is the leaf cuticular micromorphology character set, as utilized below.

8.3.2.a. Association Coefficient Groups

The *a priori* groups used were those established by cluster analysis of association coefficients for all 35 characters. The phenograms produced from euclidian distances between OTUs from discriminant analysis duplicate the groups produced from association coefficients, and are therefore not presented. This indicates that the groups established on the reduced number of characters selected as significantly discriminating by discriminant analysis, do accurately reflect the groups established on all 35 characters.

Grouping as *Araucaria* (OTUs 1,2) versus *Agathis* (OTUs 3-15) is confirmed by 8 characters. Groups established by association coefficients for all OTUs (Fig.8.1.a) are confirmed by 7 characters. Groups established without *Agathis seymouricum* (OTUs 1-14, Fig.8.1.b) are confirmed by 6 characters. Groups established for the OTUs not clearly distinguished (OTUs 4,6,8-14, Fig.8.1.c) are confirmed by 6 characters.

8.3.2.b. Whitmore Species Groups

When all 15 OTUs were grouped according to the synonymy indicated by Whitmore's treatment, only the two *Araucaria* species (OTUs 1,2), *Agathis australis* and *A.seymouricum* (OTUs 3,15), and *A.lanceolata* and *A.sp.* "R. Bleue" (OTUs 5, 7), form clearly defined groups confirmed by only 4 characters (Figs.8.2.a and 8.3, and Table 8.3). Misclassification of 5 OTUs occurred, shifting OTUs 4, 9 and 13 to the "ovata" group, and OTUs 10 and 12 to the "macrophylla" group.

When the two *Araucaria* species are removed from the analysis (Fig.8.2.b) significant grouping was established for "australis" and "lanceolata" groups, confirmed by only 3 characters. Again, 5 OTUs were misclassified, OTUs 6,9 and 13 being shifted to the "robusta" groups and OTUs 8 and 11 to the "ovata" group.

When the groups "australis" and "lanceolata" were removed (leaving OTUs 4,6,8-14) and "F-to-enter" was retained at the usual value of $F=4.0$, no characters could be selected as significant in

characterising groups. However, when "F-to-enter" was reduced to $F=2.0$, three groups were established on 4 characters, these groups corresponding exactly with Whitmore's synonymy for these OTUs (Fig.8.2.c and Table 8.1).

This allows identification of one of the two specimens from New Caledonia held in the CANU herbarium whose specific identity had not been previously determined. *Agathis* sp."R. Bleue" (OTU 7) is grouped with *A.lanceolata* (OTU 5) both by association coefficient analysis and by discriminant analysis and is therefore accepted as being conspecific. *Agathis* sp."Mt Mou" (OTU 6) is grouped with *A.vitiensis* "N" (OTU 13) by association coefficient analysis. However the restriction of *A.macrophylla* (under which species *A.vitiensis* is reduced to synonymy by Whitmore) to Melanesia renders the placing of OTU 6 in that species implausible. The strong grouping of OTU 6 with OTU 10 (*A.ovata*) by discriminant analysis (Fig.8.2.c), together with its New Caledonian origin, suggest that *A.sp.*"Mt Mou" may be conspecific with *A.ovata*. However this can only be confirmed when the cuticles of the New Caledonian species not included in this study (*A.corbassonii*, *A.montana* and *A.moorei*) have been similarly analysed.

Similarly, although OTU 9 (*A.obtusa*) groups with OTU 10 (*A.ovata*) by association coefficient analysis, discriminant analysis indicates it is more closely allied with the "macrophylla" group, OTUs 8,13,14, thus concurring with Whitmore's conclusion that *A.macrophylla*, *A.obtusa* and *A.vitiensis* should be united (see Whitmore 1980, p.45 for male cone morphology, p.46 for resin chemistry).

8.3.2.c. Page Leaf Groups

Page (1980) established three major groups on leaf external micromorphology which are here referred to as Page's A grouping. However he indicated (Page 1980, Table 1, p.76) that certain species within these groups were "very close". This "subdivision" of leaf groups 1 and 2 was used to establish 5 groups, here referred to as Page's B grouping (Tables 8.1 and 8.3). For both analyses, the "Araucaria" group was omitted.

With Page's A grouping, all OTUs are correctly classified using 4 characters (Table 8.3). However the phenogram produced from Mahalano-bis D square values (Fig.8.2.d) suggests that *A.palmerstonii* (OTU 11) is closely associated with *A.obtusa* (OTU 9) and that these form a distinct subgroup of Page's Leaf Group 2. This has occurred because OTU 11 is an outlier of the "robusta"

group and OTU 9 is an outlier of the "macrophylla" group, and they are closer to each other than to the means of their respective groups.

With Page's B grouping all OTUs are correctly classified using 6 characters (Table 8.3). Note, however, that OTU 14 had, *a priori*, been placed in the group "macrophylla" (group 2 of Page's B grouping) with OTU 8, when it would more correctly have been placed in the group "ovata" (group 2a of Page's B grouping) with OTUs 6,9,10,13. This placement was made because it maintained OTU 8 as a member of a group rather than as an entity for the purposes of calculation. This is justified by the close association of these two taxa in all other analyses. The phenogram produced (Fig.8.2.e) shows that group 3, "australis", and group 1a, "lanceolata", are clearly differentiated from each other and from the remainder. Group 2, "macrophylla", is clearly differentiated from groups 1, "robusta", and 2a, "ovata", but the latter two are only slightly differentiated from each other.

8.3.3. Characters and Character States.

The order of selection of characters by stepwise discriminant analysis for particular groupings is given in Table 8.3. This shows that the characters most frequently selected for the various groupings are abaxial cell width mean (character 20), stomatal orientation (character 26) and arrangement of subsidiary cells (character 31). The remainder, although they may be important to a particular grouping, are of little significance in the other groupings. It should be noted that selection of a character is entirely dependent on the statistical differences for the grouping selected.

Attempts to identify the particular states of the characters responsible for classification by inspection of the raw data were largely unsuccessful. Those showing consistency within and uniqueness between the groups indicated are given in Table 8.4. Note that *Agathis obtusa* (OTU 9) and *A.ovata* (OTU 10) are omitted. While they form the closest pair by association coefficient analysis (19/35 characters the same or closest), they are always closely linked to differing OTUs (Fig.8.1), and do not form a consistent *a priori* group. Furthermore, these two taxa do not form a unique *a priori* group in either Whitmore's species groups or Page's leaf groups. The group "ovata" (OTUs 6,10) while it forms a distinct group, has no unique character state so is omitted from Table 8.4.

The consistent non-association of the two specimens of *A.vitiensis* (OTUs 13,14) from different localities of Fiji, together with the closer association of OTUs 4 and 11 (cultivated in Auckland, N.Z.) with each other than with OTU 12 (from N. Queensland) suggests that ecological factors are influencing the expression of some characters of individual taxa. Attempts to identify the characters, if any, which are so influenced, have thus far been unsuccessful. Of interest in any further search for such characters would be specimens of *A.robusta* from southern Queensland and of *A.atropurpurea* from northern Queensland.

Three of the characters proposed by Page (1980) were used but only one (external opening prominence) proved to be statistically useful, being able to distinguish *Araucaria* from *Agathis*.

Six of the characters proposed by Stockey and Taylor (1981) were used. Four were statistically useful. Two characters proposed by them as of possible taxonomic use (morphology of guard cell polar extension, and wax plugs) were not found in the preparations made in this study. Several of the other characters used by them were not evident in the fossil cuticle.

Eight of the characters proposed by Cookson and Duigan (1951) were used. Six were statistically useful. However the adaptation of their character states to the present study was not accomplished with certainty and the states were generally modified.

8.4 SYSTEMATICS

Order: Coniferales

Family: Araucariaceae

Genus: *Agathis* Salisbury

Agathis seymouricum sp. nov.

Holotype: CU 700.05 CL.

Collection: Upper Seymour Stream, west bank, GR S48/739074, J.D. Lovis et.al., Dec. 1978.

Diagnosis: ultimate shoot phyllotaxis spiral, leaves alternate to subopposite not abscised from axis; leaf narrow elliptic to lanceolate, base contracted but scarcely petiolate, distal end tapering to blunt symmetrical apex, veins numerous, fine; cuticle unequally amphistomatic, adaxial stomata less frequent than abaxial, normal epidermal adaxial cells almost uniform, hexagonal, stomatal orientation perpendicular, stomata scattered or in short longitudinal rows; normal epidermal abaxial cells of mixed shape, rectangular between stomatal rows, irregular polygonal within stomatal rows; stomatal orientation perpendicular or occasionally oblique; stomata in uniseriate short longitudinal rows; stomatal aperture oval, subsidiary cells 4-5 paratetracytic and staurocytic.

Other material included: Horse Flat, 123.17 (Plate 24B, juvenile twig with at least eight pairs of ovate ^{leaves in two ranks,} leaves up to 3.3 cm long, 0.6 cm. wide); Upper Seymour Stream, west bank, 700.07, two incomplete leaves, elliptic, up to 1.8 cm wide, apetiolate; 700.08 three incomplete leaves, elliptic, up to 1.2 cm wide, apex obtuse; 711.03 ovate leaf, 5.7 cm. long, 1.2 cm. wide, cuticle examined; 712.15 one incomplete leaf, apex obtuse, cuticle examined; 712.19 leaf incomplete, 1.5 cm wide, cuticle examined; Upper Seymour Stream, east bank, 742.20 two incomplete leaves, elliptic; 742.21 one leaf ovate, 2.5 cm long, 1 cm wide; 742.23 ovate leaf, 7.0 cm long, 1.4 cm. wide, cuticle examined; 750.07 one incomplete leaf 5.5 cm long, 1.8 cm wide; 750.16/2 cuticle examined.

Plates 24A&B, 25A,C&E, 26A,C&E, 27A,C&E.

Derivation: from Seymour Stream, the locality where the holotype was found.

Description: the holotype (Plate 24A) is an ultimate shoot which is unbranched and of indeterminate growth (main stem unknown). It has spiral phyllotaxis. The leaves are alternate to subopposite, not bent or twisted at their bases, and not abscised from the axis.

~~The~~ Leaves are coriaceous, narrow elliptic to lanceolate, 2-5.5 cm long, 0.5-1.2 cm wide, and widest in their proximal part. The base is contracted but scarcely petiolate. The distal end tapers to a blunt symmetrical apex. ^{The} Veins are numerous, fine, forked near the leaf base but then unbranched, becoming parallel and then converging towards the apex but outer veins end by meeting the margins at an acute angle.

The cuticle is of medium and regular thickness, is pale under the light microscope and is unequally amphistomatic. Normal adaxial epidermal cells are of almost uniform hexagonal shape. They are 12-40 (mean = 22.5) μm long, 11-25.5 (mean = 19.6) μm wide and are arranged in files. They have thick, rounded anticlinal flanges which lack ornament. The stomata are scattered or in short longitudinal rows, perpendicularly oriented, and less frequent than on the abaxial surface. Normal abaxial epidermal cells are of mixed shape, being rectangular between stomatal rows, but irregularly polygonal within stomatal rows. They are 23-56 (mean = 38.2) μm long, 16-30 (mean = 23.3) μm wide and are arranged in files. They have thick, rounded anticlinal flanges which lack ornament. The stomata are in uniseriate short longitudinal rows, are perpendicularly or occasionally obliquely oriented, and often are not separated by ordinary epidermal cells. Stomatal rows regularly alternate with three- to five-cell wide non-stomatiferous bands. Stomatal Index = 6.7.

The stomatal aperture is oval. There are four to five subsidiary cells which are paratetracytic and staurocytic. Intercellular flanges between subsidiary cells are thin and steep. The flanges between guard cells and subsidiary cells are large, circular, coming to a point towards the poles, and nearly covering the subsidiary cells except at the poles. The inner stomatal ledges are strong, project inwards, and extend beyond the stomatal flanges at the poles.

Agathis clarencianum sp. nov.

Holotype: CU 300.32 Cl

Collection: East Quail Flat, G.R. S41/744146, J.D.Lovis et al., Dec.1978.

Diagnosis: leaves apparently abscised from axis, leaf linear - lorate to narrow oblanceolate, base gradually contracted scarcely petiolate, distal end quickly contracted to asymmetrical rounded apex, veins few usually obvious; cuticle hypostomatic, normal adaxial epidermal cells rectangular to polygonal, normal abaxial epidermal cells rectangular between stomatal rows, irregular polygonal within stomatal rows; stomata oriented perpendicular or occasionally oblique, in uniseriate rows up to four rows per interveinal band; stomatal aperture oval, subsidiary cells 4 brachyparatetracytic.

Other material included: Alexander McKay Terrace, 212.08a(1), 220.08a(1), 220.25b; East Quail Flat, 310.09, 310.13^{*}, 310.15; Lower Seymour Stream, 613.01b; Upper Seymour Stream, 700.10^{*} (Plate 24F, juvenile twig with at least eight pairs of lorate leaves), 718.32^{*}, 718.34, 718.37, 718.55a, 718.75^{*}, 750.16/1, 750.26, 750.29, 750.33, 751.30(back); (cuticle examined of all except those marked ^{*}).

Plates 24D&E, 26B,D&F, 27B,D&F.

Derivation: from Clarence River, the locality where the holotype was found.

Description: the leaves were apparently abscised from the axis except in a juvenile ultimate shoot (700.10) which has an expanded base with at least four pairs of linear leaves ^{in two ranks, and} which is itself apparently abscised.

Leaves are coriaceous, linear-lorate to narrow oblanceolate and sometimes curved. They are 4.5 - 13.0 cm long, 0.4 - 1.8 cm wide, and widest in their distal part. The base is gradually contracted but scarcely petiolate. The distal end is quickly contracted to an asymmetrical, rounded apex. Veins are few, usually obvious, unbranched and parallel, with the outer veins ending in the margins at an acute angle.

The cuticle is of medium but irregular thickness, dark under the light microscope, and hypostomatic. Normal adaxial epidermal cells are of mixed shape, being rectangular to polygonal. They are 30 - 100 (mean = 49.75) μm long, 20 - 40 (mean = 24.75) μm wide and are arranged in files. They have thin, straight anticlinal flanges which lack ornament. Normal abaxial epidermal cells are of mixed shape, being rectangular between stomatal rows and irregular polygonal within stomatal rows. They are 40 - 100 (mean = 62.86) μm long, 20 - 35 (mean = 22.6) μm wide and are arranged in files. They have thin, straight anticlinal flanges which lack ornament. Stomata are in uniseriate rows, are perpendicularly or occasionally obliquely oriented, and often are not separated by ordinary epidermal cells. Stomatal rows regularly alternate with two- to three-cell wide non-stomatiferous bands, with up to four stomatal rows per interveinal band. The stomatal bands are separated by up to 9-cell wide veinal bands. The Stomatal Index is 16.6.

The stomatal aperture is oval. There are four subsidiary cells which are brachyparacetrachytic. The intercellular flanges between subsidiary cells are thin and steep. The flanges between guard cells and subsidiary cells are moderate, oval, rounded towards the poles, and do not cover the subsidiary cells.

The inner stomatal ledges are moderate, project inwards, and do not extend beyond the stomatal flanges at the poles.

8.5 Comparisons of *Agathis* Taxa Studied

8.5.1. Comparison of *Agathis seymouricum* and *A. clarencianum*

A. seymouricum and *A. clarencianum* are distinctly different in their leaf occurrence, macromorphology and cuticular micromorphology (Plates 24,26&27).

1. *A. seymouricum* occurs as shoots with leaves attached in a spiral. Few leaves have been found detached. This suggests it was not deciduous. In contrast, *A. clarencianum* has been found only as separate leaves except for the foliage spur (700.10) interpreted as a juvenile. The leaves occur in large numbers forming "leaf banks" in muddy sediments. They are randomly oriented on the bedding planes, and occur in numerous horizons within any particular lithologic unit. This suggests a locally abundant tree which was seasonally deciduous. Sandstone crevasse splay deposits have few, scattered leaves.
2. The leaf of *A. seymouricum* is narrow elliptic to lanceolate with length/width ratio 5.5 or less, symmetrical apex, quickly contracting base and venation which is obscure except in juveniles which occur as foliage spurs, whereas the leaf of *A. clarencianum* is linear-lorate to narrow oblanceolate with length/width ratio 8.0 or more, asymmetrical apex, gradually contracting base and (usually) obvious veins.
- 3 The cuticle of *A. seymouricum* indicates that the adaxial epidermal cells were hexagonal with broad intercellular flanges, whereas the cuticle of *A. clarencianum* indicates that the adaxial epidermal cells were rectangular^{to polygonal} with narrow intercellular flanges.
4. *A. seymouricum* stomata are paratetracytic and staurocytic with 4 - 5 subsidiary cells and large, circular, pointed flanges between guard and subsidiary cells which overlap the subsidiary cells, whereas *A. clarencianum* stomata are brachyparatetracytic with 4 subsidiary cells and moderate, oval, rounded flanges between guard and subsidiary cells which do not extend far over the subsidiary cells.

5. *A.seymouricum* stomata are arranged in short, irregular, uniseriate rows on the abaxial surface and are scattered and in short rows on the adaxial surface, whereas *A.clarencianum* stomata are arranged in long, regular rows with up to four rows per band on the abaxial surface only. In the latter, broad non-stomatiferous bands indicate the position of veins.

8.5.2. COMPARISON of *Agathis seymouricum* WITH EXTANT SPECIES

The use of numerical taxonomy has allowed comparison of a fossil cuticle with those of extant species of the same family and determination of its most probable relationship within a genus. *Agathis seymouricum* and the 12 specimens of extant *Agathis* studied may be distinguished from broad-leaved *Araucaria*, including *Araucaria* sect. *Columbea* (see Stockey and Ko, 1986), by stomatal location (equally amphistomatic in *Araucaria* except in larger leaves of *A. bidwillii*, unequally amphistomatic or hypostomatic in *Agathis*) and stomatal alignment (all parallel in broad-leaved *Araucaria*, oblique or perpendicular in *Agathis*) together with 7 other epidermal characters (see Table 8.3, col.1).

Within the genus *Agathis*, division of species on cuticle micromorphology closely parallels the species recognised by Whitmore (1980) on microsporophyll and male cone morphology, at least for those of the southwest Pacific region. The leaf groups of Page (1980) are upheld but internal cuticular characters are of greater importance than external characters. The study has shown that, at least amongst the extant species of *Agathis* studied, *A. seymouricum* is closest to *A.australis*, but is nevertheless sufficiently different to deserve separate specific status (Plate 25).

Both *A.seymouricum* and *A.australis* are most closely allied to the Queensland and New Caledonian species investigated. This correlates with the geographic location of New Zealand on the eastern seaboard of Gondwana in Early/mid Cretaceous times and suggests that *A.australis* is little differentiated from *Agathis* ancestral stock.

A more extensive study of the full range of extant species, including their range of ecological variation, is clearly desirable if confident identification of any unknown specimen is to be made solely from cuticular micromorphology.

The leaves of *A.seymouricum* are similar in form to those of *A.australis*, but though longer than the adult of the latter they are shorter than the juvenile leaf.

In cuticular micromorphology *A.seymouricum* agrees with *A.australis* in:-

1. cell dimensions, especially adaxial and abaxial maximum
cell length, and abaxial mean cell width.
2. adaxial and abaxial interstomatal band cell shape
and anticlinal wall pattern and ornamentation.
3. alignment of cells in abaxial interstomatal bands.
4. stomatal location.
5. number of stomatal rows per band.
6. number of files of cells in interstomatal bands.
7. number and arrangement of subsidiary cells.

A.seymouricum differs from *A.australis* in:-

8. perpendicularly oriented, oval stomata in irregular rows
in the former compared with obliquely oriented
circular stomata in random arrangement in the latter.
9. hexagonally arranged adaxial cells in the former compared with
mixed arrangement in the latter.
10. well aligned cells in interstomatal bands in the
former compared with poorly aligned cells in the latter.
11. large, circular flanges between guard and subsidiary cells
in the former compared with small elongated flanges
in the latter.

A.seymouricum and *A.australis* may be compared with the extant *Agathis* spp. studied by utilizing the following characteristics:-

- a. generally smaller cell dimensions distinguishes these two from all other taxa.
- b. unequally amphistomatic conditions distinguishes these two from all other taxa except *A.palmerstonii*.
- c. perpendicular orientation of stomata of *A.seymouricum* agrees with those of all Queensland and Pacific Islands taxa except for *A.lanceolata* which is oblique as in *A.australis*.
- d. stomatal arrangement is random only in *A.australis*.
A.seymouricum, *A.brownii*, *A.palmerstonii* and *A.vitiensis* from the Fiji lowlands have stomata irregularly aligned in short rows.

The stomata of the remaining taxa, *A.lanceolata*, *A.macrophylla*, *A.obtusa*, *A.ovata*, *A.robusta*, *A.vitiensis* from the Fiji highlands and the two previously unidentified specimens of *Agathis* from New Caledonia are arranged in regular rows.

8.5.3. COMPARISON of *Agathis seymouricum* and *A.clarencianum* WITH OTHER FOSSIL SPECIES

In attempting to correlate the Clarence fossil specimens with previously named material, the state of nomenclature of New Zealand fossil araucariaceans was found to be so confused (as also noted by Mildenhall 1970 and Mildenhall & Johnston 1971) that a review is felt necessary. This confusion is exacerbated by Ettingshausen having in some cases described under the same name different organs (leaves, cone scales and wood) not always even from the same locality. Thus *Dammara oweni* included leaves and a cone scale from Shag Point, a cone scale from Malvern Hills and wood from Amuri. I accept the recommendation of Mildenhall (in Mildenhall & Johnston 1971, p. 68) that these Ettingshausen names be restricted to the leaves only, and follow this principle here. It should be noted,

in passing, that the woods of *Agathis* and *Araucaria* are so similar that they cannot be distinguished with certainty (Greguss, 1955; Jane, 1970). Furthermore, the "family has morphologically uniform pollen. *Agathis* pollen is smaller than that of *Araucaria*, but the size ranges overlap" (Martin 1978, p.187). No examination of cuticle of New Zealand fossil species of *Agathis* has previously been made.

Ettingshausen (1887) described three species of *Agathis* (= *Dammara*) from the Upper Cretaceous of New Zealand, namely *Dammara oweni* and *D. uninervis* from Shag Point, Otago, and *D. mantelli* from Pakawau, northwest Nelson. For all three species, the leaf material illustrated is very limited (Ettingshausen 1887, PL.I, Figs.20,22-24 and PL.VII, Fig.20) but it can nevertheless be said that the external features of *Agathis seymouricum* generally agree with those of *D.mantelli* Ett. except in the leaf apex, which is obtuse as in *D.oweni* Ett. *A.clarencianum* is unlike any of them.

Agathis jurassica White, previously known as *Podozamites lanceolatus* (Etheridge, 1889; Walkom, 1921) has been described from the Jurassic Talbragar Fish Bed flora of New South Wales. It has "leaves lanceolate, when mature between 4 and 7 cm long, maximum width between 0.5 - 0.75 cm, arranged in a lax spiral on foliage spur branchlets with 20 - 40 leaves. Each leaf has 5 - 8 parallel veins." (White, 1981, p.700). Its cuticular micromorphology is unknown. *A.seymouricum* differs from *A.jurassica* in both leaf dimensions and arrangement, although the foliage spurs described here as juvenile approach *A.jurassica* in both characters. Leaves of *A.clarencianum* are of similar length to those of *A.jurassica* but are wider and of different form. The fossil described here as a juvenile foliage spur of *A.clarencianum* (700.10)^(Plate 24.F) approaches that illustrated by White (1981, Fig.3) and said to be of the "*Podozamites gracilis*" type (loc.cit. p.701).

Two species of *Agathis* were described by Cookson and Duigan (1951) from Victoria; *Agathis yallournensis* from Yallourn, and *Agathis parwanensis* from Baccus Marsh. Both are Tertiary in age. Data for the two Australian fossils were obtained from Cookson and Duigan (1951) Table 4 and their descriptions. Additional data were measured from (loc.cit.) Plate 4, Figs.33 & 34, and Plate 6, Figs.46 & 47.

Data for *A.australis*-(my data), *A.australis*-(C. and D. data), *A.seymouricum*, *A.parwanensis* and *A.yallournensis* for 13 characters are given in Appendix 3⁴. Cluster analysis shows that *A.seymouricum* is more similar to *A.australis*-(my data) than to either of the Australian fossil species (Fig.8.4.a). However,

with so few characters involved, little weight should be given to this clustering as evidenced by the dissimilarity indicated between *A.australis*-(my data) and *A.australis*-(C. and D. data). That dissimilarity highlights the difficulties involved in choice of characters, and in adapting data of other authors to one's own interpretation of character states.

A.seymouricum differs from *Agathis parwanensis* in stomatal location, cell size and subsidiary cell arrangement although the stomatal orientation and arrangement in rows is similar.

A.seymouricum differs from *A.yallournensis* in leaf form and is of larger dimensions. *A.yallournensis* is said to have veins "frequently inconspicuous" (Cookson and Duigan, 1951, p.432), but judging from their Plate 4, Figs.28 - 32, they are considerably more conspicuous than those of *A.seymouricum* which are deeply buried in leaf tissue. Their cuticular micromorphology is somewhat similar (e.g. both unequally amphistomatic and with paratetracytic and staurocytic subsidiary cell arrangement) but differ^s in stomatal orientation and arrangement in rows, the number of stomatal rows per band, and the shape of cells in interstomatal bands.

Data for *A.australis*-(my data), *A.australis*-(C. and D. data), *A.seymouricum*, *A.clarencianum*, *A.parwanensis*, *A.yallournensis* and *A.robusta* for 32 characters are given in Appendix 3. Cluster analysis shows that *A.clarencianum* and *A.parwanensis* are the most similar (Fig.8.4.b). *A.seymouricum* and *A.australis* are the next most similar pair but they are clustered markedly separate from *A.clarencianum*, *A.parwanensis* and *A.yallournensis*. When the extant Australian species *A.robusta* is included to test any Australian influence (Fig.8.4.c), it clusters with *A.seymouricum* and *A.australis* while the other three remain clustered as before. Thus, *A.clarencianum* is most similar to Australian Tertiary species, while *A.seymouricum* is most similar to extant species and in particular *A.australis*, for which it is the most likely ancestor.

A.clarencianum agrees with *A.parwanensis* in cell dimensions, stomatal location and orientation, and subsidiary cell arrangement but differs in stomatal arrangement in rows and number of stomatal rows per band and in number of subsidiary cells.

A.clarencianum agrees with *A.yallournensis* in leaf form (cf. Plate 24 D with Cookson and Duigan, 1951, Pl.4, Figs.28-32) even though *A.yallournensis* is described as being "narrow- to broad-lanceolate" (Cookson and Duigan 1951, p.432). The leaf abaxial cell dimensions and stomatal

arrangement in rows are similar but they differ in adaxial cell dimensions, stomatal location and orientation, and in subsidiary cell number and arrangement.

8.6.DISCUSSION

8.6.1. Taxonomic Value of Cuticular Characters in *Agathis*

As indicated above, Whitmore (1980) considers leaf macromorphology to be inadequate to distinguish most species of *Agathis*. However both Page (1980) and Stockey & Taylor (1981) agree that some taxonomic division may be possible using cuticular micromorphology.

The taxonomic usefulness of particular cuticular characters appears to depend on the taxonomic level at which they are used. Thus at the generic level, *Agathis* may be distinguished from *Araucaria* sect. *Columbea* by 8 characters (see Table 8.4). The most useful of these are stomatal location and orientation.

At the specific level, species may be differentiated by a total of 13 characters, but the character(s) which may be useful varies between species groupings. Thus the "australis" group (plus *A.palmerstonii*) possess few stomata on the adaxial surface and many on the abaxial surface, the "lanceolata" group and *A.australis* have stomata obliquely orientated, the "robusta" group and *A.obtusa* have random abaxial cell alignment, the "macrophylla" and "vitiensis" groups (and "Araucaria") have only paratetracytic arrangement of subsidiary cells, and the "australis" and "vitiensis" groups lack adaxial anticlinal cell wall ornamentation. Thus only by the use of as many characters as possible may an unknown OTU be allied with its most probable species group.

The present study shows that clear distinctions may be made between the cuticular characters of *A.australis* (N.Z.), *A.robusta* (Queensland) and species of the islands of the south-western Pacific. The cuticular characters of Whitmore's Group A species and of Malesian species of Group B are at present unavailable for comparison.

One of the characters used in this study demands special discussion in view of its taxonomic importance and use by previous workers. The classification of *Agathis* species on the orientation of

stomata as defined by Cookson and Duigan (1951, p.434) has not been upheld by either Stockey and Taylor (1981) or the present study (see Table 8.1). The character states used here do not rely on the precise measurement of angle or percentages. Rather, the general trend of the majority of stomata in relation to the veins of the leaf is used. Thus "parallel" refers to most stomata being parallel to veins, "perpendicular" refers to stomata mostly parallel to each other and approximately perpendicular to veins, and "oblique", refers to stomata mostly at varying angles between parallel and perpendicular to veins.

8.6.2. The earliest *Agathis*

Stockey (1982) has recently provided a valuable review of the records of fossil Araucariaceae which supplements that of Miller (1977). Several early records of supposed *Agathis* are now recognised not to be even araucariacean. Stockey concludes that acceptable records of *Agathis* are confined to the Southern Hemisphere and are Tertiary in age.

Several characters serve to distinguish *Agathis* from *Araucaria* (see Stockey, 1982). In *Agathis*, the bract and ovuliferous scale are completely fused into one cone scale, while in *Araucaria* the bract and ovuliferous scale are only partially fused. Seeds of *Agathis* are winged and separate from the scale when shed. *Araucaria* has seeds that are deeply embedded in scale tissue and are never removed from the scale except in the case of *Araucaria bidwillii*. The leaves of *Agathis* are broad and flattened with rounded tips and narrowed bases. The leaves of *Araucaria* are sharply pointed, needle-like and imbricate in some species or broad and imbricate, usually with a keel and an acute tip, in others. The leaf cuticle of *Agathis* shows stomata arranged in random, irregular or regular rows on the abaxial surface and in some species on the adaxial surface as well. Orientation varies from parallel, to oblique, to perpendicular, but is most often oblique or perpendicular. The leaf cuticle of *Araucaria* varies with leaf morphology. Those species with broad imbricate leaves have regular rows of stomata on both surfaces. The stomata are oriented parallel to the leaf margin. Those species with needle-like imbricate leaves have widely spaced rows of stomata on both surfaces and some leaves show discontinuous rows or groups of stomata. The stomata are oriented parallel or oblique to the leaf margin.

Any or all of these features may be impossible to distinguish in fossil material depending on the material fossilised and its state of preservation. In particular, the bract/ovuliferous scale character,

obvious enough in living material, is rarely seen in fossil material, which may indeed also present a misleading appearance due to weathering (e.g. *Cycadeostrobus brunonis*, Stockey 1982,p.140).

With respect to *Agathis jurassica*, White (1981, p.697) simply writes, without further elaboration, that the associated cone scales are "undeniably of *Agathis*", but Stockey (loc.cit.p.143) states "they also show close similarities to those of *Araucaria* sect. *Eutacta*". I am not able to offer an opinion. However in writing (loc.cit.) of the foliage shoots that "the deciduous foliage spurs are also diagnostic of the genus" White is in error. This feature is surely characteristic of *Agathis*, but is not diagnostic, since similar behaviour is shown by *Araucaria*. Since no cuticular information is available and, as Stockey writes (loc.cit.p.150), "Affinities of foliage without cuticle remains in doubt", the generic attribution of *A. jurassica* must, for the time being, remain controversial.

Agathis seymouricum and *A.clarencianum* are the only Mesozoic fossils for which leaf cuticle characteristic of *Agathis*, as distinct from *Araucaria*, has been demonstrated. However, in the light of this demonstration of *Agathis* in the New Zealand Early Cretaceous, it is reasonable to presume that some, at least, of the New Zealand Late Cretaceous macrofossils attributed to *Agathis* (or *Dammara*) do belong to that genus.

8.6.3. Centres of dispersal?

Agathis seymouricum and *A.clarencianum* occur in strata that were laid down prior to the commencement of the separation of New Zealand from Gondwana in Late Cretaceous time. The fossil record shows that at least in Cretaceous times both extant ^{ae}araucarian genera were present in New Zealand. Since mid Tertiary times *A.australis* is the only remaining descendant chronospecies of a diverse assemblage of araucariaceans, one of which was the distinct species *A.seymouricum* from which *A.australis* has, most probably, directly evolved.

In developing their hypothesis that "*Agathis* has invaded the Malay archipelago and the Melanesian islands from two Gondwanic centres" [in north Queensland and New Caledonia], Whitmore and Page (1980, p.415) take no account of fossil evidence. Though the two migratory directions they postulate are in broad terms plausible, it seems undeniable that these two geographic centres of diversity are essentially latter-day refugia and not necessarily centres of dispersal. The timing of these migrations

is not specified, nor is it known, and may well relate to a relatively early date when this genus (and *Araucaria*) were both more diverse in taxa and in distribution in eastern and northern Australia. To focus on these two persisting refugia may, therefore, be a mistake.

9.1. Introduction

The only formally described and illustrated angiospermous fossil leaves from the Cretaceous Period of New Zealand are those described by Franz Unger(1864), Baron Constantin von Ettingshausen(1887,1891) and Laurent (in Arber,1917). James Hector(1880,1886a) listed many names and illustrated three named (1886b) and many unnamed (Hector, "Unpublished Plates") angiospermous leaves, all of which have been adjudged invalid by Mildenhall(1970). The age of two dicotyledonous species invalidly named by Crie(1889) is unknown.

Unger(1864) described five species of dicotyledonous leaves from Late Cretaceous sediments at Pakawau, Nelson (Gregg, 1971,p.261) and placed them all in the form genus *Phyllites*.

Ettingshausen(1887,1891) described a total of 37 new dicotyledonous species in 26 genera. Most of the species were referred to modern European genera. Only seven generic names were modified by suffixes suggesting affiliation rather than direct descent. He placed all genera in modern families. Various authors (Nagelhard,1922; Oliver,1950; Oliver in Couper,1953; McQueen,1956) have informally referred eight of Ettingshausen's species to different genera, some of which are modern Southern Hemisphere genera, e.g. *Fagus ulmifolia* Ett. referred to *Nothofagus* by Oliver(1950). One species of monocotyledon leaf, *Haastia speciosa* Ett., was formally referred to the new genus *Pakawaua* by Mildenhall(1972a).

These fossils described by Ettingshausen came from various localities:- Shag Point (23 spp. of dicotyledon, one sp. of monocotyledon), Pakawau (nine spp. of dicotyledon, two spp. of monocotyledon), Malvern Hills I (five spp. of dicotyledon, three of which also occur at Shag Point), Cave Stream, also known as Murderer's Creek, and Trellissic^k Basin (four spp. of dicotyledon, three of which also occur at Shag Point) and Weka Pass (one sp. of dicotyledon). The age of sediments at all of these localities is Late Cretaceous (Upper Senonian to Maastrichtian) (Mildenhall,1970,1972b; Gregg,1971).

Laurent (in Arber,1917,Pl.14a,b) described one species of dicotyledon leaf thought by Arber to be from Early Cretaceous (Neocomian) sediments at Waikato Heads but now known to have come from Late Cretaceous sediments at Pakawau (McQueen,1955).

Hector(1880,1886a) used an array of European and Southern Hemisphere modern genera, plus new form genera with modern connotations, e.g. *Fagus*, *Metrosideros*, *Kaikomako*, *Ranunculites*. Many of the fossils to which Hector applied names were housed in the Canterbury Museum (Gregg,1971) and were undoubtedly included in the collection sent to Ettingshausen in 1884. Thus different names were probably applied to the same fossil. This is indicated by the approximation of certain names and figures in Hector's "unpublished plates" with those of Ettingshausen(1887). Thus *Kohekohe dysoxyloides* Hect.(1880,"unpub.pl.", Pl.21, Fig.28) is probably the same as *Diospiros novae-zeelandiae* Ett.(1891, Pl.28, Fig.4). Kohekohe is the Maori/common name for *Dysoxylum spectabile* (Forst.f.) Hook.f.,the only extant New Zealand member of the Meliaceae (mahogany family). *Diospiros* is a member of the Ebenaceae (ebony family) none of which now occur in New Zealand. Compare also Hect."unpub.pl.",Pl.21, Fig.34 with Ett.(1891),Pl.28,Fig.13.

All of the Cretaceous dicotyledon fossils illustrated by Unger, Hector and Ettingshausen were collected prior to 1885 when Alexander McKay first visited Quail Flat in the middle Clarence valley and subsequently reported the presence of dicotyledonous leaves (McKay,1886; see Introduction for fuller details). Thus McKay's Clarence fossils were neither described nor illustrated. However Hector (1886a) made use of four of McKay's fossils in the Indian and Colonial Exhibition in London in 1886, two of them, *Fagus grandifolia* Hect. n.n. and *Phyllites purchasi* Unger, being dicotyledons. He also referred to the collection in a footnote to Juhl's translation of Ettingshausen's 1887 paper (Ettingshausen, 1891, p.242). Here Hector refers to the leaves as *Fagus (ninnisiana ?)* Unger and *Protophyllum* sp. though earlier, in the Exhibition Catalogue (Hector, 1886a) he had referred the *Protophyllum* to *P.purchasi* Unger. Both *F.ninnisiana* and *P.purchasi* were based on leaves from Late Eocene (Bartonian) sediments at Drury. Hector(1886a) applied the name *P.purchasi* to fossils not only from Quail Flat but also from Collingwood, Pakawau, Malvern Hills I and Waikato. This species was transferred to *Pisonia* by Penseler(1930). Possible correlations of these names with leaves described here are indicated below.

9.2. Character Definition and Choice

Mayr (1969, p.413) defines a taxonomic character as "any attribute of a member of a taxon by which it differs or may differ from a member of a different taxon." Sneath and Sokal (1973, p.71) point out that "characters are restricted to differences between members of taxa, but the taxa cannot be recognised without the characters themselves being first known."

Hickey (1973) and Doyle (1974) outlined a system for describing angiospermous leaf architecture using continuous, ordered discrete (multistate qualitative), non-ordered (multistate qualitative) and binary characters. Some of their characters have states which are not mutually exclusive. Characters used in this study which are not defined in this section follow the definitions of Doyle (1974).

Hill (1980) dealt with the choice of characters of angiosperm leaves with a view to their use in numerical taxonomy especially for fossil floras. He stressed the need for the use of quantitative characters especially (a) continuous characters based on a ratio scale and (b) binary characters. He (loc.cit.p.228) decided that since the main effect of adding characters with high ($r > 0.6$) correlation was to isolate the species further, they should be used "since the new information in each character outweighs any negative effect of high correlation between characters." Sneath and Sokal (1973, p.106) suggest that even highly correlated characters should be included since they assumed at least some independent sources of variation in any empirical correlation. Rohlf (1967) claimed that the only effect of high character correlation was to elongate the phenetic clusters. However Blackburn (1981,p.10) said that consideration of character correlations "are important for the distortions of character space they produce." He selected an arbitrary significance value for correlation coefficients of $r = 0.7$, one of a pair of characters having a greater correlation being excluded. Blackburn also stressed the need to choose ordered, multistate, qualitative character states such that they were not only "hierarchical but also that the difference between them can be considered to be equal"(loc.cit.p.10). However, Gower's coefficient of similarity (Gower,1971) permits the use of continuous, ordered discrete, non-ordered and binary characters and allows for missing data.

In the present study it is considered desirable to use continuous characters where possible but other character types are also included. It may be argued that some of the characters classified as "ordered discrete" do not have states such that the differences between them can be considered equal

(i.e. a non-linear scale). However the states are considered to be of equal taxonomic difference within this particular set of leaves and are therefore treated as Type Three for Gower's Coefficient. The binary characters used are Type Two for Gower's Coefficient because shared negative states are counted as similarities.

9.2.1. Shape

The problems of measuring leaf shape as a character have been addressed by a number of authors. The major problem lies in quantifying the arbitrary outline shapes generally used for descriptive taxonomy (Hickey, 1973). Fisher (1960) used the relative diameter (width/length) to represent the marginal curve in studies of geographic variation of leaf shape in *Ranunculus insignis*. Dilcher (1974) used "balance" of the whole lamina and of the base only plus lamina "form". Balance was described as symmetrical or asymmetrical. Lamina form was divided into four states, oblong, elliptic, ovate and obovate. Each of these states was subdivided into classes delimited by particular values of the length/width ratio. Hill (1980) devised a character set for a numerical taxonomic approach to the study of angiosperm leaves from a collection of extant species. To describe shape, he (loc.cit.p.217) used the ratio length/width plus a complex "leaf shape index" measured by use of a standard grid based on the distance from the midrib of leaf margin segments delimited by angular displacement. This grid was also used (loc.cit.p.224) to estimate the "modified length" of incomplete leaves, this modified length being substituted for total length where required. Blackburn (1981) used the ratio length/width in his descriptions of podocarp leaves and the lobes of *Banksiaephyllum*. Cantrill and Webb (1987, p.73), in distinguishing species of *Phyllopteroides*, calculated shape as the "distance from the base of the pinnule to the point of maximum width divided by the total pinnule length" and plotted this ratio against pinnule width. West and Noble (1984) used a number of characters derived from digitised leaf images to analyse the *Dodonaea viscosa* complex. Leaf shape was expressed as a number of continuous characters derived from direct and computational measurements including the ratios length/width and position of maximum width (see below), as well as leaf area, perimeter, and symmetry, a "form factor" and a "leaf

shape index". The position of maximum width was defined by the ratio distance from apex to point of maximum width/total leaf length, both measured along the midrib.

The intrinsic problem with using a ratio to express shape is that the use of both numerator and denominator as well as their ratio as separate characters replicates information thus "weighting" characters. To choose the most suitable ratio characters to represent lamina shape, the unpublished work of Frampton (1988) is used here. Frampton has shown that the more normal of the two potential ratios formed from two continuous characters is the form with the ratio of the coefficients of variation (c.v.) of the constituents greater than one. Having thus established the choice of numerator and denominator, the numerator is then omitted from the character set. This is to avoid the duplication of information that naturally occurs when a ratio and its two constituents are all included in a data set. Normality of the data, as indicated by the univariate measures of skewness and kurtosis, should thus be maximised as part of the character choice so that the normality assumption for many parametric tests is more likely to be met.

In the present study, three measurements associated with shape were obtained, viz. (1) length of midrib (L) from insertion of the petiole (base) to the apex measured along the midrib (Fig.9.1,AB), (2) width at widest point (W) measured perpendicular to the midrib (Fig.9.1,CD), and (3) distance from the base to the widest point (BTOW) measured along the midrib (Fig.9.1,BE). If the lamina meets the petiole at different heights on each side of the midrib, the point of insertion is taken as midway between the two lamina/petiole junctions. Six ratios are thus possible for complete leaves. The number of ratios possible is reduced for incomplete leaves, the actual number for a particular leaf depending upon the presence of apex or base. Using the data of 102 leaves from the nine multi-character form species, all of the means, coefficients of variation, skewness and kurtosis were calculated for the three primary characters and the six ratios formed from them using BMDP2D programme (Table 9.2). The preferred variables are W, BTOW, L/W and L/BTOW (see Section 9.4.1.a.ii for details of selection). The ratios L/W and L/BTOW are similar to those used by West and Noble (1984).

These characters are also used in the analysis of the numerotypes of the 22 form species. In addition, the maximum length of midrib recorded within a form species plus lamina "balance" and "form" as defined by Dilcher (1974) are used. Maximum length is included because for three form species no leaves have been found whole, therefore L, L/W and L/BTOW are all missing values. But both length

and shape are important taxonomic characters in this leaf set, so some representation of length is desirable. Furthermore, the numerotype (from which the ratios are calculated) is not always the longest leaf of a particular form species. Eight form species have at least one leaf longer than the numerotype.

Lamina "balance" is expressed as a two-state character. West and Noble (1984) were able to express leaf symmetry as a continuous character using the ratio of the lengths of the left and right margins because of their digitalization of leaf images.

Lamina "form" is here expressed by using the ratio $L/BTOW$ to classify leaves as obovate (<1.75), elliptic ($1.75-2.3$), ovate (>2.3) or oblong (<1.75 and >3.0) and the ratio L/W to specify their subdivision as defined by Dilcher (1974, p.19; see also Fig.9.2). The combination of both ratios gives a non-ordered, multistate qualitative character. This character has a relatively high correlation with lamina width ($r=0.476$) and basal angle ($r=0.568$) but both of these are within Blackburn's (1981) recommended value. Correlations with its constituents (L/W and $L/BTOW$) are surprisingly low ($r=-0.255$ and $r=0.345$ respectively), probably as a consequence of the use of many character states.

Area, as defined by Dilcher (1973), was considered for inclusion but was omitted from the cluster analysis because it had high ($r>0.7$) "logical" correlations with L , W and $BTOW$. With respect to the choice of ratios to express lamina shape (L/W and $L/BTOW$), it is noteworthy that area had low correlations with them ($r=0.117$ and $r=0.565$ respectively), despite derivation from common elements. Thus although the same primary characters (L , W) are used, different character bases must be being expressed.

9.2.2. Base

Descriptive taxonomy uses a non-ordered multistate character to define the basal shape of the lamina. Thus Dilcher (1974, p.21), having defined the base of the lamina as "that portion of the leaf bounded by approximately the lower 25% of the margin", classified the base according to its angle (acute or obtuse) together with its shape (normal, cuneate or decurrent), or alternatively as one of seven special shapes. Dolph (1976a,b) adopted this strategy and defined 14 separate character states.

Hill (1980, p.217) defined the basal angle as "the angle between the lines joining the intersections with the margin of the axis of 20% maximum width basally and the base" to obtain a continuous character.

The definitions of both Dilcher and Hill for basal angle require the presence of a complete leaf. Furthermore, they are difficult to apply to asymmetric, decurrent or lobed leaf bases, and fail to establish the size of basal lobes if present. The problem of an asymmetrical, lobed leaf base was addressed by Dancik and Barnes (1974) in their study of leaf diversity in yellow birch (*Betula alleghaniensis*). They used three characters viz. base symmetry (symmetrical or asymmetrical), base shape of longer side (cordate, subcordate, truncate, rounded to obtuse, or cuneate to acute) and degree of cordateness (measured as the distance from the point of insertion of the petiole to the tangent to the basal lobe drawn perpendicular to the petiole).

In the present study basal angle is defined as the maximum angle attained by the tangents from the point of insertion of the petiole on the lamina to the margins (Fig. 9.1, the angle measured within the leaf between FB and GB where B is the point of insertion of the petiole). If the lamina meets the petiole at different heights on each side, the point of insertion is taken as midway between the two lamina/petiole junctions. This definition includes information about the lamina which is excluded from the leaf length character in a leaf where the lamina extends beyond the point of insertion of the petiole, i.e. has basal lobes. It could thus be considered to be one of a number of characters defining leaf shape. Additional characters, basal balance and basal shape describe the relationship of the lamina to the petiole in the region immediately adjacent to the point of insertion of the petiole.

9.2.3. Apex

Definitions of the apex by Dilcher (1974) and Hill (1980) are similar to their respective definitions of the base. Difficulties of application similar to those given above in respect of the base are again encountered.

In the present study apical angle is defined as the minimum angle attained by the tangents from the apex to the margins in the apical region of the leaf (Fig. 9.1, the angle measured within the leaf

between HA and IA). This allows meaningful measurements to be made even when the apex itself is missing (which is common in fossils with an attenuate apex) or when the leaf is bilobed.

This is the only apical character used in analysing the multi-character form species because all of the leaves except three have acute or attenuate apices. For cluster analysis of the 22 numerotypes, apical shape based on five ordered discrete states (Section 9.3) is included and apical angle omitted. It was necessary to exclude one of the two characters because they are logically correlated. Indeed their correlation coefficient is high ($r=0.847$). Apical shape was preferred to apical angle because it had a lower coefficient of variation. It also allows description of the shape of the apex which is not immediately apparent from the continuous character apical angle. Thus distinction between an attenuate apex and an acuminate apex with equal apical angle is possible. It may be with other data that the apical angle may be preferable to apical shape.

9.2.4. Venation

Hickey (1973) and Dilcher (1974) used continuous, ordered discrete and non-ordered characters to describe several orders of venation in angiosperm leaves. Hill (1980) used a complex system of relative vein width to identify the hierarchy of vein orders and to distinguish between secondary and intersecondary veins. He used the number, length, and relative angles of secondary veins, areoles and ultimate veinlets to establish numerous continuous characters. He acknowledged (loc.cit.p.224) some of his characters "will be impossible to measure on most fossils due to lack of preservation of ultimate venation patterns." Furthermore, he stated (loc.cit.p.216) that "without using extremely involved definitions, it is impossible to define accurately vein orders higher than secondaries. For many palaeobotanical studies any veins finer than secondaries or intersecondaries are often unreliable; so it is proposed that higher vein orders should not be used as primary characters in fossil studies."

In contrast, Dilcher (1974,p.14) states "The classification of fossil specimens using gross leaf form without considerations of fine venation and/or cuticular characters, produces unreliable results" and stresses the point when he continues "gross leaf form and gross venation patterns, when studied in

conjunction with fine venation and cuticular characters, can provide very reliable information about the fossil record of angiosperm leaves." Furthermore, third and higher order venation patterns are an integral part of the taxonomic treatment of dicotyledonous leaves by Hickey and Wolfe (1975).

Coalified fossils of membranaceous leaves from the Clarence valley show excellent preservation and presentation of all vein orders. However, coalified fossils of chartaceous or coriaceous leaves, and natural surface ^{impressions} present great difficulty in observing not only the finer venation but also in measuring the width of veins. Therefore, the characters used here are modifications of those of Dilcher (1974) which are visible and are considered to be of taxonomic value. All of the leaves described here are simply pinnate, and vein orders higher than third order are either absent or not easily visible; therefore only characters involving second and third order veins are included, together with one describing areolar development. Most are non-ordered characters (Section 9.3).

First order veins (primaries) are here defined as the thickest order of veins in a leaf which arise from the petiole, diminish in thickness across the lamina and terminate at or near the apex and lobe apices of simple leaves. Paired veins of equal thickness to the midrib but arising from it above the insertion of the petiole (suprabasal acrodromous, actinodromous or palinactinodromous of Doyle, 1974) are also considered to be primaries. In compound pinnate leaves there is one primary. In compound palmate leaves there is one primary per leaflet.

Second order veins (secondaries) are here defined as those major veins which arise from the primary vein (midrib) in a relatively regular pattern and which diminish in thickness across the lamina. In campylodromous, acrodromous or actinodromous leaves (Dilcher, 1974), with more than one primary vein, they may arise from one or all of the primary veins but do not pass from one primary to another. Secondaries may terminate (simple craspedodromous) or not terminate (camptodromous) at the margin. When a secondary vein branches just within the margin, one branch may terminate at the margin while the other branch joins the superadjacent secondary (semicraspedodromous). Veins not terminating at the margin may loop to join the superadjacent secondary (brochidodromous), gradually diminish exmedially as they curve towards the apex without forming prominent loops (eucamptodromous), freely ramify towards the margin (cladodromous) or repeatedly branch into a vein reticulum (reticulodromous). The Clarence leaves commonly exhibit combinations of these venation patterns.

When this is so, the most prevalent pattern in the basal two-thirds of the leaf is taken as typical since the upper one-third of most of the leaves is narrower, restricting the development of vein patterns.

Eight of the form species described here have secondaries which loop to join the superadjacent secondary (see Dilcher, 1974, p.42). Seven of these which have loops joining at right angles also have tertiary loops enclosing these loops. The one form species with loops joining at an acute angle has no enclosing tertiary loops, giving a correlation coefficient for the characters SECLOOP and TERTLOOP of $r=1.0$. Although this correlation is not "logical", the secondary vein loop angle character was omitted from cluster analysis because of the large number of "no comparisons" its inclusion would have entailed. Furthermore, looping of secondaries is, in part, included in the character VEINTYP (see Section 9.3).

Intersecondary veins are intermediate in thickness between that of second and third order veins. They arise from the midrib, are more or less regularly interspersed between the secondaries and do not extend as far across the lamina as do the secondaries. They may be a single vein segment (simple) or made up of coalescing tertiary veins for over 50% of their length (composite).

Third order veins (tertiaries) are here defined as those minor (intercostal) veins which arise from primary and/or secondary veins in a regular pattern and which maintain constant thickness across the lamina. They may branch into higher orders without rejoining the secondaries (ramified), anastomose with other tertiary veins (reticulate), or join tertiary veins from the adjacent primary or secondary vein (percurrent). Subclasses of these patterns and other characters associated with tertiary vein configuration including angle of origin are detailed in Dilcher (1974). Higher vein orders are distinguished from tertiary veins by being finer and by forming a more or less closed mesh within the tertiary vein pattern.

Areoles are defined by Dilcher (1974, p.50) as "the smallest areas of leaf tissue surrounded by veins which taken together form a contiguous field over most of the area of the leaf." They may be well developed, imperfect, incompletely closed or lacking. They may be enclosed by tertiary veins or by higher order veins. They may contain ultimate veinlets.

9.2.5. Secondary Vein Angle

Dilcher (1974, p.38) described the secondary vein "angle of divergence" as being "measured above the point of divergence" and divides it into five discrete states, narrow acute ($<45^\circ$), moderate acute (45-

65°), wide acute (65-80°), right angle (80-100°), and obtuse (>100°). Hill (1980, p.218) defines two separate secondary vein angles, one relating to the admedial section, the other to the exmedial section of the secondary vein, and employs them as continuous characters. The difficulty in using Hill's "secondary vein angle a" in the present study lies in locating the position of the adaxial 10% length of a secondary vein without determining its total length (see above). Also, the variation in vein angle is accommodated by Hill simply by averaging the angles of all secondary veins. As Dilcher (1974, p.38) recognised, leaves show consistent variation in angle of divergence up, and/or across the leaf. This variation is accommodated here by the character "secondary vein angle variation" (see Character States, Section 9.3).

One of the states of Dilcher's (1974, p.39) "variation in angle of divergence" character is "more acute on one side of the leaf than on the other". This state could be treated as a separate character. In this study, three of the multi-character *a priori* form species appeared to exhibit this state. Therefore, in the preliminary data analysis, the different angles from "left" and "right" sides of the leaf were expressed as "minimum" and "maximum" vein angles respectively. The correlation coefficient for these two characters is $r=0.94$. For leaves with approximately equal angles laterally, use of both would duplicate information. One should therefore be deleted from the character set used for cluster analysis. Vein angle maximum has a lower coefficient of variation and is less skewed (see Table 9.2), so was preferred for cluster analysis.

Secondary vein angle is here defined as the maximum angle attained between the midrib and the tangent to the secondary vein through the point of origin of the secondary vein. If the angles of individual secondary veins within a leaf vary by more than (an arbitrary value of) 5°, the variation is expressed as the non-ordered character "secondary vein angle variation".

9.2.6. Secondary Vein Course

Under this heading, Dilcher (1974, p.40) included course (straight, or sinuous or zigzag), curvature (uniform, abrupt, or recurved), and branching (branched or unbranched) of secondary veins. Since one or other of the states of all three will occur in the same leaf, they are here treated as separate characters with additional states for curvature and branching, plus the additional character "secondary vein arrangement".

The course of a secondary vein (Fig.9.3) is considered to be "straight" when vein segments maintain a consistent course across the lamina, even though the whole vein may curve. The course is considered "sinuous" or "zigzag" when vein segments show an irregular course, changes in direction being respectively gradual or abrupt. It can be difficult to distinguish between the latter two states, so they may be treated as one state.

Description of the curvature of a secondary vein across the lamina (Fig.9.3) involves consideration of the whole of the secondary vein. Vein curvature may be (i) straight, (ii) uniformly curved, (iii) abruptly curved, (iv) gradually increasing in curvature up the leaf, (e.g. from straight at the base to curved at the apex), (v) gradually decreasing in curvature up the leaf, (vi) organised so that upper veins curve up while lower veins curve down (implying straight central veins), or (vii) recurved. The state "recurved" was placed in the character VEINCURV in this study because initial investigations of characters followed Dilcher (1974). In hindsight, it may have been better placed in the character VEINCORS.

Secondaries may branch equally or unequally (Fig.9.4). Equal branching is evident when vein segments beyond the point of branching are of equal thickness and diverge at approximately equal angles to the vein segment before the point of branching, forming a Y junction. Unequal branching has vein segments beyond the point of branching of unequal thickness, the thinner branch curving away from the thicker branch while the thicker branch continues the course of the vein segment before the point of branching. Thinner branches may diverge above (upper) and/or below (lower) the thicker branch.

Secondaries show consistent arrangement over the whole leaf (Fig. 9.4) giving intercostal areas of characteristic shape. They may be converging, approximately parallel or diverging. Hill (1980, p.218) used a similar character defined by the ratio length of secondary/distance between secondaries measured along the primary.

9.3. Character States

The characters and their states detailed below ^{either} were selected from those listed by Dilcher (1974) and are marked with a \$, or were established from their occurrence in the fossils studied in this investigation. Those selected from Dilcher (1974) do not always include all of the states listed by him, inclusion and/or modification being governed by their occurrence in the fossils. Those established here are defined in the previous section under the appropriate character definitions. The characters used for parametric analysis, cluster analysis and discriminant analysis are indicated in Table 9.1.

1. Length (L) of midrib from apex to petiole insertion measured along the midrib (Fig.9.1, AB). For analysis of 102 individual leaves the length of midrib of complete leaves is used for discriminant analysis but omitted from cluster analysis (see Section 9.2.1). For analysis of 22 numerotypes, the length of midrib of the longest leaf, complete or incomplete, from each form species is used.
2. Maximum lamina width (W) measured perpendicular to the midrib (Fig.9.1, CD).
3. Position of maximum lamina width (BTOW) calculated as the distance from the point of petiole insertion to the widest point of the lamina measured along the midrib (Fig.9.1, BE).
4. Lamina shape as described by the ratio length/width (L/W).
5. Lamina shape as described by the ratio length/ base to widest point of the lamina (L/BTOW).
- 6 \$. Lamina area (AREA) as described by Dilcher (1973), excluded from cluster analysis of 22 numerotypes (see Section 9.2.1); 1 = microphyll, 2 = notophyll, 3 = mesophyll.
- 7 \$. Lamina Form (FORM) Fig.9.2; 1 = narrow oblong, 2 = oblong, 3 = narrow obovate, 4 = wide obovate, 5 = very wide obovate, 6 = narrow elliptic, 7 = elliptic, 8 = elliptic/narrow ovate, 9 = narrow elliptic/lanceolate, 10 = lanceolate, 11 = narrow ovate, 12 = ovate.
- 8 \$. Lamina Balance (LAMBAL); 1 = symmetrical, 2 = asymmetrical.
9. Basal angle (BASE) Fig.9.1, the angle FBG.
- 10 \$. Basal balance (BASBAL); 1 = symmetrical, 2 = slightly asymmetrical, 3 = asymmetrical, 4 = very asymmetrical.
- 11 \$. Base shape (BASHAPE); 1 = decurrent, 2 = cuneate, 3 = normal.

12. Apical angle (APEX) Fig.9.1, the angle HAI, excluded from cluster analysis of 22 numerotypes (see Section 9.2.3).
- 13 \$. Apex Shape (APEXSHAP); 1 = attenuate (drip tip), 2 = acute, 3 = rounded, 4 = obtuse, 5 = emarginate.
- 14a \$. Margin (MARGIN), for analysis of 102 individual leaves; 1 = entire, 2 = slightly wavy, 3 = wavy, 4 = erose.
- 14b \$. Margin (MARGIN), for analysis of 22 numerotypes; 1 = entire, 2 = slightly crenate, 3 = coarsely crenate, 4 = lobed, 5 = obtuse serrate, 6 = acutely serrate. Combinations are coded as means e.g. entire/slightly crenate = 1.5.
- 15 \$. Marginal glands (HYDATHOD) which are here determined as hydathodes; 1 = absent, 2 = present.
- 16 \$. Lamina texture (TEXTUR); 1 = very membranaceous, 2 = membranaceous, 3 = chartaceous.
- 17 \$. Secondary vein type (VEINTYP); 1 = simple, 2 = semicraspedodromous, 3 = cladodromous, 4 = eucamptodromous, 5 = brochidodromous. Combinations of these states are used to establish nine states in the analysis of ¹⁰² individual leaves.
- 18a. Secondary vein angle (VEINMIN), (see Section 9.2.5), used only in the analysis of 102 individual leaves.
- 18b. Secondary vein angle (VEINMAX), (see Section 9.2.5).
- 19a \$. Secondary vein angle variation (VEINVAR), for analysis of 102 individual leaves, lowest pair weak, more acute; 1 = absent, 2 = present.
- 19b \$. Secondary vein angle variation (VEINVAR), for cluster analysis of 22 numerotypes; 1 = uniform, 2 = lowest pair more acute, 3 = more acute on one side, 4 = upper more obtuse, 5 = upper more acute, 6 = irregular.
- 20 \$. Secondary vein thickness (VEINTHIK) relative to primary vein thickness; 1 = fine, 2 = moderate, 3 = thick, 4 = very thick.
21. Secondary vein branching (VEINBRAN) Fig.9.4; 1 = none, 2 = lower only, 3 = upper and lower, 4 = equal.
- 22 \$. Secondary vein course (VEINCORS) Fig.9.3; 1 = straight, 2 = sinuous or zigzag.

- 23a \$. Secondary vein curvature (VEINCURV) Fig.9.3, for analysis of 102 individual leaves; 1 = straight, 2 = abrupt, 3 = uniform.
- 23b \$. Secondary vein curvature (VEINCURV) Fig.9.3, for cluster analysis of 22 numerotypes; 1 = straight, 2 = uniform curve, 3 = abrupt curve, 4 = increasing curvature up the leaf, 5 = upper curve up/ lower curve down, 6 = recurved.
24. Secondary vein arrangement (VEINARR) Fig.9.4; 1 = converging, 2 = approximately parallel, 3 = diverging.
- 25 \$. Secondary vein loops (SECLOOP), excluded from cluster analysis of 22 numerotypes (see Section 9.2.4), join superadjacent secondary vein; 1 = acutely, 2 = at right angles. For discriminant analysis a third state, "do not loop", would have to be instituted to accommodate "no comparison", which would make the character multi-state, non-ordered. Such a character type is not able to be used in discriminant analysis.
- 26 \$. Secondary vein loops enclosed by tertiary vein loops (TERTLOOP); 1 = not enclosed, 2 = enclosed.
- 27 \$. Intersecondary veins (INTERSEC): 1 = absent, 2 = simple, 3 = composite.
- 28 \$. Tertiary vein angle of origin (TERTANGL), exmedial side first; 1 = acute/acute, 2 = acute/right angle, 3 = right angle/acute, 4 = right angle/right angle, 5 = obtuse/right angle.
- 29 \$. Tertiary vein pattern (TERTPATN); 1 = random reticulate, 2 = orthogonal reticulate, 3 = percurrent.
- 30 \$. Areoles (AREOLES); 1 = well developed, 2 = imperfect, 3 = incompletely closed, 4 = lacking.

9.4. Results

9.4.1. Form Species

Synopsis

Twelve of the form species established have a single character, or a combination of two or three characters which clearly differentiate them from other forms. A further nine form species were established on a combination of four or more characters (see Section 3.3.2.c).

Analysis of the data for 16 characters (see Appendix 3.6) diagnostic for these nine multi-character a priori form species allows the classification of all but one of the 102 leaves measured, only 33 of which were complete. One of the nine *a priori* form species discussed in this section was initially thought to be capable of subdivision by separation of five OTUs but is now shown to be a coherent group. Each leaf whose *a priori* classification was placed in doubt by analysis was reinspected before accepting or rejecting reclassification.

Three of the leaves (OTUs 34,39,40) cannot be assigned to any of the *a priori* form species. Two of these (OTUs 39, 40) are described as separate form species. The third is incomplete so cannot be adequately described and remains incertae sedis. 15 leaves which initially were not easily assigned to one or other of two alternative choices amongst the form species were confidently assigned after analysis. Four leaves (OTUs 6,42,46,54) were shown to belong to form species other than those to which they were initially assigned.

9.4.1.a. Parametric Analysis for Numerotype and Character Selection

(i) Numerotype Selection

The group mean, standard error (S.E.), and coefficient of variation were calculated for the continuous characters L, W, BTOW, BASE, APEX, VEINMIN, and VEINMAX (see Table 9.2). The *a priori* assignment of OTUs was analysed using two different groupings.

Grouping 1 incorporates the initial assignment of OTUs to the nine multi-character form species, informally named "ellipt", "obov", "octo", "panax", "gris", "ovata", "diosp", "cunites", and "atten". However, 15 OTUs (10,12,16,17,46, 48,60,61,63,66,69,70,87,88,93) were initially not easily assigned to one or other of two alternative choices amongst the form species. Grouping 2 incorporates their alternative assignments. It has nine groups informally named "ellipt", "obov", "octo", "gris", "ovata", "diosp", "cunites", "atten" and "myrica". The only two OTUs (39,40) initially placed in "panax" are transferred to "diosp" thus eliminating the former *a priori* form species. The group "myrica" contains the five OTUs (5,7,9,18,21) suspected of being a subgroup of "ellipt". However, cluster analysis indicates that for the majority of OTUs, the clustering of Grouping 1 is more satisfactory than the clustering of Grouping 2. Therefore, the latter is abandoned. Individual OTU assignments are given in Section 9.4.1.b.

listed in Table 9.2

From the parametric analyses, the complete leaf closest in values for these characters to the group mean in Grouping 1 was selected as ^apossible numerotype for the form species. Those selected are "ellipt", OTU 13; "obov", OTU 30; "octo", OTU 35; "panax", OTU 39; "gris", OTU 41; "ovata", OTU 50; "diosp", OTU 56; "cunites", OTU 80; and "atten", OTU 98.

(ii) Character Selection

The mean, S.E., ^ccoefficient of variation, skewness and kurtosis were calculated for the same characters as in (i) above together with the six ratios possible from L, W, and BTOW for all 102 OTUs. Results are presented in Table 9.2.

Of the six possible ratios, the three ratios showing lower skewness and kurtosis for each pair are L/W, W/BTOW and L/BTOW. To avoid duplication of information by using all three primary characters with their derived ratio characters at least one of the primary characters should be removed from the data set. Removal of L and retention of L/W and L/BTOW retains significantly more variation than removal of either of the ratios. This allows the use of both W and BTOW as additional characters in cluster analysis without excessive duplication of information.

The characters VEINTYP and VEINBRAN are excluded from discriminant analysis because they are multi-state and non-ordered. The exclusion of VEINMIN from cluster analysis is discussed in Section 9.2.5.

9.4.1.b. Cluster Analysis

(i) Complete Data Set

Association coefficients of the 102 OTUs listed in Appendix 3.6 for the 14 characters listed in Column 2 of Table 9.1 are calculated using Gower's coefficient, and the resultant matrix subjected to cluster analysis using unweighted arithmetic average linkage using the MINT6 program (Rohlf, 1971). The resultant phenogram is presented as Fig.9.5.

Seven major clusters are formed, one of which is subdivided. Cluster 1 (27 OTUs, 1-77, Fig.9.5) contains all of the leaves assigned *a priori* to "diosp" except for OTUs 65 and 66, together with leaves assigned *a priori* to "ellipt" (OTUs 1,6,22), "octo" (OTU 38), and "panax" (OTUs 39,40). Cluster 2 (20 OTUs, 2-25, Fig.9.5) contains only leaves assigned *a priori* to "ellipt" except for one (OTU 42) assigned *a priori* to "gris". Cluster 3 (17 OTUs, 20-31, Fig.9.5) may be subdivided into two subclusters. Cluster 3a (10 OTUs, 20-80, Fig.9.5) contains all the leaves assigned *a priori* to "cunites" (OTUs 78 to 82 inclusive) together with leaves assigned *a priori* to "ellipt" (OTUs 20,21,24) and "diosp" (OTUs 65,66). The leaves assigned *a priori* to "ellipt" and "diosp" form a tight group within Cluster 3a and are discussed below. Cluster 3b (7 OTUs, 26-31, Fig.9.5) contains all the leaves assigned *a priori* to "obov". Cluster 4 (4 OTUs, 33-37, Fig.9.5) contains all the leaves assigned *a priori* to "octo" except for OTUs 34 and 38. Cluster 5 (12 OTUs, 41-50 Fig.9.5) contains all the leaves assigned *a priori* to "ovata", except OTU 46, together with two leaves assigned *a priori* to "gris" (OTUs 41,43). Cluster 6 (2 OTUs, 34,36, Fig.9.5) contains two leaves assigned *a priori* to "octo" and "ovata" respectively. Cluster 7 (20 OTUs, 83-97, Fig.9.5) contains all the leaves assigned *a priori* to "atten" (OTUs 83 to 102 inclusive).

Nineteen leaves whose clustering places their *a priori* assignment to form species in question are discussed below. Their *a priori* assignment is given in () brackets. The seven OTUs removed from the data set used for further cluster analysis are indicated by an asterisk.

OTUs 1 and 22 ("ellipt") form a distinct group within Cluster 1 which is dominated by "diosp". While sharing some characters with "diosp", their general shape and venation type give no reason to reclassify them.

OTU 6 ("ellipt") lies within the main "diosp" cluster. It has the general appearance of "ellipt" but lacks the apex. It has eucamptodromous secondaries and weak basals which are more acute and after reinspection is reclassified as "diosp".

OTUs 20, 21 and 24 ("ellipt") together with OTUs 65 and 66 ("diosp") form a distinct group within Cluster 3a. OTUs 20 and 24 are undoubtedly "ellipt". OTU 21 is reclassified as "cunites" by discriminant analysis (see below). "Cunites" has a symmetrical, cuneate, wide acute base while "ellipt" has an asymmetrical, decurrent, obtuse base. OTU 21 has an asymmetrical, decurrent, 115° base so is left in "ellipt".

OTU 34* ("octo") and OTU 46 ("ovata") form the loose but distinct Cluster 6. OTU 34 lacks an apex and has a mixture of characters which prevent it from being assigned to any of the form species established and remains incertae sedis. It is therefore removed from the data set for further cluster analysis of form species.

OTU 38 ("octo") clusters with "diosp", presumably because it has eucamptodromous venation and weak basal secondaries.

OTU 39* ("panax") clusters in "diosp" but has distinctive brochidodromous secondaries and symmetrical lamina and base so cannot be assigned to any of the *a priori* groups. It is described as a separate form species, *Proteaceaphyllum lanceatum* sp.nov., and is therefore removed from the data set for further cluster analysis of form species.

OTU 40* ("panax") clusters in "diosp" but has distinctive brochidodromous secondaries and symmetrical lamina and base so cannot be assigned to any of the *a priori* groups. It is described as a separate form species, *Proteaceaphyllum oblongum* sp.nov., and is therefore removed from the data set for further cluster analysis of form species.

OTUs 41* and 43* ("gris") cluster, together with OTU 54("ovata"), as a group within Cluster 5 "ovata". They have distinctive apex and base characteristics and eucamptodromous secondaries and are described as a separate form species *Parvifolium emarginatum* sp.nov. They are therefore removed from the data set for further cluster analysis of form species.

OTU 42 ("gris") is in Cluster 2 "ellipt". It has semicraspedodromous venation, zigzag secondary vein course and hydathodes which suggest it does belong in "ellipt".

OTU 46 ("ovata") and OTU 34 ("octo") form the loose but distinct Cluster 6. OTU 46 lacks a base but has semicraspedodromous venation, lower branching of secondaries and hydathodes which suggest it actually belongs in "ellipt".

OTU 54 ("ovata") clusters, together with OTUs 41 and 43 ("gris"), as a group within Cluster 5 "ovata". It lacks a base so lacks the majority of the continuous characters.

OTUs 65* and 66* ("diosp"), together with OTUs 20, 21 and 24, form a distinct group within Cluster 3a "cunites". OTU 65 lacks an apex so lacks the majority of the continuous characters. The base is typical of "diosp" but lacks weak basal secondaries. It is accepted as an unusual "diosp" but removed from the data set for further cluster analysis of form species. OTU 66 is a difficult leaf with many characters typical of "diosp" but has a wide very asymmetric base and no weak basal secondaries. It is accepted as an unusual "diosp" but removed from the data set for further cluster analysis of form species.

OTUs 93 and 97 ("atten") form a distinct subgroup of Cluster 7 "atten", perhaps because they are the only leaves assigned *a priori* to "atten" which have "lower" rather than "equal" branching of secondaries. Otherwise they are typical of the form species. Only OTU 97 is reclassified as "cunites" by discriminant analysis (see below). "Cunites" has a symmetrical, cuneate, wide acute base while "atten" has an asymmetrical, decurrent, obtuse base. OTU 97 has an asymmetric decurrent 93^o base so is left in "atten".

(ii) Reduced Data Set

The same procedure as outlined in (i) above is used for the 95 OTUs remaining after the removal of outliers (Appendix 3.6 [reduced set]). The resultant phenogram is presented as Fig.9.6. The removal of outlier OTUs which cause disturbance of a character-defined hyperspace has been shown to be justified by Frampton (1988). Removal of OTUs from the data set causes reassignment of numbers to OTUs. For simplicity in presentation, the original OTU numbers are retained here while the "new" numbers (i.e. those in Fig.9.6) are given in [] brackets.

Five major clusters are formed, two of which may be subdivided. Cluster 1 [25 OTUs, 1-70, Fig.9.6] contains only leaves assigned *a priori* to "diosp" except for OTUs 1 [1] and 22 [22] ("ellipt") and 38 [37] ("octo"). Cluster 2 [31 OTUs, 2-73, Fig.9.6] may be subdivided. Cluster 2a [21 OTUs, 2-38,

Fig.9.6] contains only leaves assigned *a priori* to "ellipt". Cluster 2b [10 OTUs, 20-73, Fig.9.6] contains all the leaves assigned *a priori* to "cunites" together with some of those assigned *a priori* to "ellipt" (OTUs 20 [20] and 21 [21]), "ovata" (OTU 54 [49]), and "atten" (OTUs 85 [78] and 90 [83]). Cluster 3 [11 OTUs, 26-36, Fig.9.6] may also be subdivided. Cluster 3a [7 OTUs, 26-31, Fig.9.6] contains all the leaves assigned *a priori* to "obov". Cluster 3b [4 OTUs, 33-36, Fig.9.6] contains all the leaves assigned *a priori* to "octo" except OTU 38 [37]. Cluster 4 [10 OTUs, 39-41, Fig.9.6] contains all the leaves assigned *a priori* to "ovata" plus OTU 46 [41](?"ellipt"). Cluster 5 [18 OTUs, 76-90, Fig.9.6] contains only leaves assigned *a priori* to "atten".

OTUs 1 [1] and 22 [22] ("ellipt") still form a distinct group within Cluster 1. There is no obvious reason why they do not cluster with "ellipt". While OTU 22 [22] lacks a base and is therefore a difficult leaf to classify, OTU 1 [1] appears to be quite typical of "ellipt" ^{regardless of the outcome of the numerical analysis} so their assignment is not changed.

OTU 6 [6] was reclassified as "diosp" and still clusters in exactly the same manner as before removal of outliers.

OTUs 20 [20] and 21 [21] ("ellipt") now form a subgroup with OTUs 85 [78] and 90 [83] (see below) in Cluster 2b perhaps because they lack hydathodes. OTU 20 [20] is undoubtedly "ellipt". OTU 21 [21] could be "cunites" except for its asymmetric base so is left as "ellipt".

OTU 24 [24] ("ellipt") is now well within Cluster 2a "ellipt".

OTU 38 [37] ("octo") still clusters within Cluster 1 "diosp". Its secondaries, however depart at different angles on either side of the midrib so is accepted as "octo".

OTU 42 [38] ("gris"), suspected of belonging in "ellipt", now clusters in Cluster 2a "ellipt" and is accepted as such.

OTU 46 [41] ("ovata") suspected of belonging in "ellipt" still lies close to but distinct from Cluster 4 "ovata". It is accepted as an unusual "ellipt".

OTU 54 [49] ("ovata") now clusters with "cunites" and is reclassified as such.

OTUs 85 [78] and 90 [83] ("atten") occurred as a subgroup within the "atten" cluster in Fig.9.5. They now cluster with OTUs 20 [20] and 21 [21] within Cluster 2b. OTU 85 [78] lacks the basal 2/3 and OTU 90 [83] lacks the apical 1/3 of the leaf, but the characters congruent with those of "cunites" (cladodromous venation, uniform curve of secondaries, entire margin, no hydathodes) give insufficient evidence to justify reclassification. They are therefore accepted as "atten".

OTUs 93 [86] and 97 [90] ("atten") remain as a subgroup within Cluster 5 "atten".

9.4.1.c. Discriminant Analysis

To ascertain the relative value of each of the 14 characters listed in Table 9.3 in determining the clustering of the 102 OTUs discussed in Section 9.4.1.b.i, discriminant analysis using the BMDP7M program (Dixon, 1981) was carried out. This also produces Mahalanobis D square values for each OTU relative to the means of the *a priori* groups which indicate possible misclassifications. The program only considers those OTUs which have data for all characters i.e. complete leaves, so only 33 of the 102 OTUs are used in the analysis. The numbers of complete leaves in each *a priori* group are: "ellipt" - eleven ; "obov" - one; "octo" - one; "panax" - two; "gris" - one; "ovata" - three; "diosp" - six; "cunites" - two and "atten" - six. Groups with only one OTU must have zero within-group variance for all characters and are therefore represented in character-defined hyperspace only as a point. This difficulty is overcome by using the "jackknife" option (see Section 3.3.1.b for details).

(i) Numerotypes

The group means, and the group centroids established from the coefficients of canonical functions I and II, serve to suggest which OTU of a group might be most suitable as numerotype for the group (Fig.9.7). Only those groups with three or more OTUs are considered. The numerotypes for groups with less than three OTUs are accepted as determined above (Section 9.4.1.a.i).

In Group "ellipt", OTUs 13 and 15 are closest to the group mean. OTU 15 has a narrower basal angle and wider apical angle than most in the group, and when unjackknifed was reclassified as "ovata". OTU 13 was previously suggested, and is retained as the numerotype.

In Group "ovata", OTUs 44 and 51 are closest to the group mean. OTU 44 is a leaf fragmented after deposition and is reclassified by discriminant analysis to "diosp". OTU 51, while having all characters present in the data set does not possess a complete margin, and was reclassified to "ellipt" by unjackknifed discriminant analysis. The only remaining complete leaf in the group, OTU 50, is retained as the numerotype.

In group "diosp", OTUs 55, 58 and 69 are closest to the group mean. OTU 55 is a leaf fragmented after deposition and has an apical angle wider than any other leaf classified as "diosp". OTU 58 lacks the weak basal secondaries present in most "diosp". OTU 69 is a very small leaf suspected of being an incompletely expanded, "juvenile" leaf. The next closest to the group mean is OTU 56 which is retained as the numerotype.

In group "atten", the OTUs closest to the group mean are (in order) 89, 97, 91 and 98. OTU 89 is an abnormal leaf, being curved and having a symmetrical, narrow angled base. OTU 97 is the only leaf in "atten" with simple craspedodromous venation, has lower branching secondaries and has the apex on an adjacent block. It is reclassified by jackknifed discriminant analysis as "cunites" but this is discounted (see below). OTU 91 is an abnormal leaf with one margin of the apical 1/3 of the leaf being very erose, suggesting damage during growth. OTU 98 lacks a small portion of one margin in the medial section of the leaf through subaerial erosion but is otherwise complete, and is retained as the numerotype. Indeed it was the founding leaf of the group during the initial investigation.

(ii) Characters

One character, VEINCORS, has zero within-group variance and therefore cannot be entered into the discriminant analysis. Several other characters have very low F values and would not normally be entered. This is overcome by "forcing" the program to consider all characters (see Section 3.3.1.b). The order of forced selection is VEINCURV (Character 23a, Section 9.3), BASE, APEX, L/W, VEINVAR (Character 19a), L/BTOW, BTOW, W, VEINMIN, VEINMAX, HYDATHOD, MARGIN and L. However the cumulative proportion of total dispersion for Axis 1 is 92% and for Axis 2, 96%, so most of the variability can be expressed in few dimensions, implying correlated discriminating abilities among the characters. Inspection of the standardised coefficients for canonical variables (Columns 3&4, Table 9.3) shows that Axis 1, which separates *a priori* groups "obov", "octo", and "panax" from the others (Fig. 9.7), is achieved mostly by use of the characters (in order) L/BTOW, VEINMIN, BTOW, and W. Axis 2, which separates *a priori* group "atten" and partially separates groups "obov" and "cunites", shows little emphasis on any particular character, the highest values being those for (in order) VEINMIN, VEINCURV, L/BTOW AND W.

(iii) Misclassification of OTUs

Ten OTUs are determined as misclassified by jackknifed discriminant analysis. Of these, two (OTUs 39,40 "panax") are now known to be individuals (see above) which must be assigned to separate form species. Of the remainder, only two (OTUs 21 "ellipt" and 97 "atten") were in doubt as a result of the cluster analysis (Section 9.4.1.b).

OTU 21 is reclassified by jackknifed discriminant analysis as "cunites", but because it has an asymmetric, decurrent, obtuse base it is retained in "ellipt".

OTU 97 is also reclassified by jackknifed discriminant analysis as "cunites", but it has hydathodes as well as an asymmetric, decurrent, obtuse base, so is retained in "atten".

Summary

All leaves measured except one (OTU 34) are assigned to one of ten form species. Eight of the nine form species proposed are maintained. The ninth ("panax", OTUs 39,40) is split into two form species, each containing only one leaf. Four leaves are reassigned; OTU 6 is removed from "ellipt" and placed in "diosp"; OTU 42 is removed from "gris" and placed in "ellipt"; OTU 46 is removed from "ovata" and placed in "ellipt"; and OTU 54 is removed from "ovata" and placed in "cunites". The best numerotypes are "ellipt", OTU 13; "obov", OTU 30; "octo", OTU 35; "gris", OTU 41; "ovata", OTU 50; "diosp", OTU 56; "cunites", OTU 80; "atten", OTU 98; plus the individual entities OTU 39 and OTU 40. Thus, together with the 12 form species already recognised (Section 3.3.2.c), a total of 22 form species are identified.

9.4.2 Form Genera

Synopsis

It is proposed to group the 22 form species identified above into form genera by following the same procedures as those used for grouping individual leaves into form species.

Parametric analysis of the data for 30 diagnostic characters from the numerotypes of 22 form species (10 multi-character form species established in Section 9.4.1, plus 12 form species established on one, two or three characters) shows that three of the characters have correlations sufficiently high to require their exclusion from cluster analysis. It also suggests that "best guess" values may be inserted for missing data without significantly altering the outcome of cluster analysis or discriminant analysis. However, cluster analysis using 27 characters without "best guess" values inserted for missing values serves best to establish five groups of form species on overall resemblance, and is, in part, used to assign the form species to six form genera. Discriminant analysis of 23 characters with "best guess" values included, i.e. no missing values, identifies the best discriminating characters for this grouping.

9.4.2.a. Parametric Analysis of Characters

Data for the 30 characters listed in Column 4 of Table 9.1 were obtained from the numerotype selected for each of the 22 form species established giving 22 OTUs for analysis (see Appendix 3.7). Analysis of pair-wise similarity of the characters is computed using Pearson's correlation coefficient. Table 9.4 lists the most significant correlations.

The pairs L v. AREA, W v. AREA, BTOW v. AREA, and APEX v. APEXSHAP are all logically correlated, i.e. the first of each pair is a primary character whose magnitude has a strong influence on the magnitude of the second. AREA and APEX are therefore removed from cluster analysis. Removal of AREA is indicated by its high correlation with three useful characters. Removal of APEX is discussed in Section 9.2.3.

The pairs TEXTUR v. VEINCORS, VEINTYPE v. VEINARR, VEINCORS v. TERTPATN, and SECLOOP v. TERTLOOP are "biologically" correlated, i.e. the state of the first of each pair influences the state of the second for biological (structural) reasons. Only for the last pair is it considered necessary to exclude one of the pair, the character selected for exclusion being SECLOOP (see Section 9.2.4 for discussion).

The pairs L/W v. SECLOOP and L/W v. TERTLOOP have no apparent reason, logical or biological, for being highly correlated. The correlation probably occurs because the narrowest leaf in the set (OTU 18) is the only one to have SECLOOP "acute" and TERTLOOP "not enclosed". Since SECLOOP is excluded on different grounds (see above) no further action is taken.

The data matrix contains missing values either because the numerotype is not complete or because a form species does not possess a certain character. The characters SECLOOP and TERTLOOP fall into the latter category and account for 28 missing values. In cluster analysis, SECLOOP is removed and TERTLOOP maintained as "no comparison" (N.C.) values for the 14 form species which do not have looped secondaries. In discriminant analysis SECLOOP is removed because it is a multi-state, non-ordered character. For TERTLOOP, those OTUs which do not have looped secondaries are given the state "not enclosed".

Of the form species with missing values attributable to incompleteness of the numerotype, one (OTU 17) lacks both base and apex, another (OTU 19) lacks the base and a third (OTU 4) lacks the apex. These account for a total of 12 missing values in the characters BTOW, BASE, APEX, L/W and L/BTOW. Three form species (OTUs 1,4,8) do not display areoles because of the chartaceous nature of the fossils. One of them (OTU 8) does not display tertiaries for the same reason.

Thus 17 missing values, or 2.58% of the data matrix, are actually missing while 28, or 4.24% of the data matrix, are missing because they are character states not present in the form species (N.C.). Since the latter are dealt with in other ways for subsequent analyses, they do not present a problem. The 17 genuine missing values would however present a problem in discriminant analysis since an OTU is disregarded if it has any missing values. Therefore "best guess" values were obtained from other leaves of the relevant form species and are underlined in Appendix 3.7.

Correlation coefficients calculated using the "best guess" values (Table 9.5) show little change. The only pairs to become significantly correlated are L v. BTOW and W v. BTOW. The importance of these characters suggests that their removal on the grounds of logical correlation is not appropriate.

9.4.2.b. Cluster Analysis

Association coefficients of the 22 OTUs for the 30 characters listed in Column 5 of Table 9.1 and Appendix 3.7 with missing values entered as no comparison (N.C.) are calculated using Gower's coefficient (1971), and the resultant matrix subjected to cluster analysis using unweighted arithmetic average linkage by means of the MINT6 program (Rohlf, 1971). The resultant phenogram is presented as Fig.9.8.

Five major clusters are formed. Cluster 1 (OTUs 1,11,8,9,10,6; Fig.9.8) contains six OTUs in three groups, 1 with 11, 8 with 9 and 10, and the least similar, 6, being the last to join. Cluster 2 (OTUs 5,7,13,12; Fig.9.8) contains four OTUs which are not closely similar to each other. OTUs 5 and 13 are the most similar within the cluster with OTU 12 the least similar and the last to join. Cluster 3 (OTUs 14,22,15; Fig.9.8) contains three OTUs which have the lowest similarity to each other of any cluster, joining at slightly greater than 0.6 similarity. Cluster 4 (OTUs 4,16,17,21,18; Fig.9.8) contains five OTUs which have low similarity to each other, especially OTU 4 (<0.6 similarity to all others in the cluster). Cluster 5 (OTUs 2,3,20,19; Fig.9.8) contains four OTUs, three of which (2, 3, and 20) are very similar to each other (>0.8 similarity), the remaining OTU (19) joining at 0.67 similarity.

When the highly correlated characters APEX, AREA and SECLOOP are removed (Fig.9.9) all but Cluster 2 remain unchanged. Similarity values are slightly lowered. For example, Cluster 5 joins the other clusters at 0.49 similarity compared with 0.50 previously. Cluster 2 now has OTUs 7 and 13 most similar with OTU 5 the next to join.

When "best guess" values are inserted for missing values for the 30 characters, (Fig.9.10), clusters remain essentially unchanged except that OTU 15 shifts from Cluster 3 to become an outlier in Cluster 1, and OTUs 8 and 9 are the most similar in Cluster 1 compared with OTUs 9 and 10 previously

(Figs.9.8,9.9). Similarity values are generally unchanged from Fig.9.8, being only slightly higher in some cases.

When the highly correlated characters APEX, AREA and SECLOOP are removed from the data matrix containing "best guess" values (Fig.9.11), OTU 15 returns to Cluster 3 (with OTUs 14 and 22), OTUs 8 and 9 remain more similar than OTUs 9 and 10, and OTUs 7 and 13 are more similar (as in Fig.9.9) than OTUs 5 and 13 (Fig.9.8), Similarity values are generally unchanged from Fig. 9.8.

The minor variations of clustering are not important since division into taxa above the species level has been applied in this study only to similarities less than 0.7. However, consideration of the placement of the form species represented by OTU 15 indicates that the data set of 27 characters without "best guess" values inserted for missing values (Fig.9.9) gives the taxonomically most sound grouping.

The relatively unchanged similarity values indicate that insertion of "best guess" values so that all OTUs will be included in the discriminant analysis is valid. However the inclusion of all characters with "best guess" values seriously displaces OTU 15. Therefore the "most sound" *a priori* grouping for discriminant analysis is that obtained by cluster analysis using the data set of 27 characters with "best guess" values inserted for missing values and is represented by Fig.9.11.

9.4.2.c. Discriminant Analysis for Characterisation of Groups.

To ascertain the value of each of the 23 characters listed in Table 9.6 in determining the clustering of the 22 OTUs discussed in Section 9.4.2.b, discriminant analysis using the BMDP7M program (Dixon, 1981) is carried out. The five *a priori* groups derived from cluster analysis using the data set of 27 characters with "best guess" values inserted for missing values (Fig.9.11) are Group 1 (OTUs 1,6,8,9,10, 11), Group 2 (OTUs 5,7,12,13), Group 3 (OTUs 14,15,22), Group 4 (OTUs 4,16,17,18,21) and Group 5 (OTUs 2,3,19,20). The order of selection of characters by "forced" discriminant analysis (see Section 3.3.1.b) is given in Table 9.6. None of the OTUs are misclassified. It is interesting to note that, in contrast, when the "jackknife" option (see Section 3.3.1.b) is used, 17 OTUs are misclassified. This suggests that removal of any individual OTU seriously disrupts the grouping.

The major characters are (in order of selection) TERTPATN, VEINARR, LAMBAL, AREOLES, INTERSEC and L. Inspection of the data for these characters (Table 9.7) indicates clearly why they effect this grouping. Thus, the distribution of character states for the most discriminating character TERTPATN are:- (1) all the OTUs in Group 5, but only they, have percurrent tertiaries, (2) Groups 1 and 3 have only OTUs with random reticulate tertiaries, while (3) Groups 2 and 4 have some OTUs with random reticulate tertiaries and some with orthogonal reticulate tertiaries. The second most discriminative character, VEINARR, shows similar distribution of states. Thus, two OTUs in Group 5 (OTUs 19,20) are the only ones with diverging veins, and all OTUs with converging veins are in Group 4. Subsequent characters show similar but less well defined distribution between groups.

However, there is no obvious basis which links these characters to morphological (? genetic) or environmental grouping influences. Thus, although the grouping is clearly defined by these characters, and outliers within groups may be distinguished by their unusual combinations of characters, this particular set of characters is of little taxonomic value above the form species level.

The cumulative proportion of total dispersion for Axis 1 is 66%, and for Axis 2 is 94%. Thus most of the variability is expressed by very few of the characters. Inspection of the data for the characters listed in Table 9.6 shows that distribution of the group means along Axis 1, which separates *a priori* Group 1 from the other groups (Fig. 9.12), is achieved mostly by the characters (in order) AREOLES, TERTLOOP, VEINARR, APEXSHAP and L. Groups 4 and 5 are separated along Axis 2 by the characters (in order) L/W, INTERSEC, TERTLOOP, APEXSHAP and VEINCORS. Again, this particular set of characters has no apparent morphological or environmental basis.

9.4.2.d Alternative Noncomputational Schemes

Hickey and Wolfe (1975,p.546) stated that the "architectural features of greatest importance in assessing systematic and phylogenetic affinities at the higher taxonomic levels are" (1) simple versus compound leaf organisation; (2) entire versus toothed margins; (3) characteristics of the tooth including shape, characteristics of the apex, occurrence and type of glandular processes, and vein configuration within the tooth; (4) major vein configuration; (5) characters of the intercostal venation including its orientation, and the presence and type of intersecondaries; and (6) gland position, including marginal,

laminar, acropetiole, etc. This suggests that these characters could be used to form coherent patterns of morphology of apparent value in determining phylogenetic affinities.

Not all of the characters used in their "Leaf Key to the Dicot Subclasses" (loc.cit. p.550) are observable in the Clarence fossils. Use of those which are determinable suggests that all of the form species described herein are located in the Subclass Magnoliidae. Consideration of the characters used by them for ordinal subdivision of the Magnoliidae is inconclusive. The only group to show any correlation of characters is Group 4 (excluding OTU 4) with simple leaves with entire margins, brochidodromous secondary venation and reticulate tertiary venation but lacking intersecondaries (except OTU 18). The presence or absence of stipules is very uncertain. These characters suggest the group may be located in the Order Laurales.

Consideration of the groups in terms of leaf rank, as described by Hickey (1971), shows that all are Rank 2 except for Group 5 which is Rank 3.

Krassilov (1977) proposed a morphological classification of early angiosperm leaves based on gross morphology. Following his descriptions, Groups 1 and 3 would be classified as ficophylls, Group 2 as ?rosiphylls, Group 4 as laurophylls and Group 5 as ?platanophylls (except that their secondary venation is pinnate not actinodromous). These "indications" have been used in constructing some of the form genera described below.

Crabtree (1987) classified the Albian to Campanian fossil leaves from the Northern Rocky Mountains as belonging to certain leaf morphotypes. None of the Clarence leaf form species correspond closely to his morphotypes. The ovate to elliptic leaves of Groups 1 and 3, which would otherwise fit into his "magnoliaephyll" morphotype lack brochidodromous secondary venation. The leaves of Group 5 could be placed in his "protophyll" morphotype except for the presence of percurrent tertiaries. OTUs 16 and 17 broadly correspond to his "cinnamomophyll" morphotype but lack transverse, regularly spaced tertiaries. Similarly, the leaves of Groups 1 and 2 with camptodromous secondaries, which could be placed in his "cornophyll" morphotype, lack transverse, regularly spaced tertiaries. The remaining eight of his 12 morphotypes are not represented among the Clarence leaves. Conversely, several of the Clarence leaves, especially OTUs 4,5,7,14,15,18,21 and 22 cannot be even remotely likened to any of his morphotypes.

Upchurch and Wolfe (1987,p.76) detailed six leaf physiognomic characters which they use to infer climatic and vegetational change with time. The characters are :

1. Leaf size, measured by a series of size classes (those of Raunkiaer, 1934, as modified by Webb, 1959).
2. Leaf margin, classified as either serrate or entire.
3. Leaf texture, classified as either thick, xeromorphic or thin, hygromorphic.
4. Drip tip, present or absent.
5. Leaf organization, classified as simple or compound.
6. Leaf shape, classified as narrow (stenophyllous) or broad, cordate (typically palmately veined) or lobed.

Consideration of the Clarence leaves in terms of these characters and of the generalised leaf types of Upchurch and Wolfe (1987, p.82) produces "some semblance of order" to the clustering. Table 9.8 details the appropriate data for their characters plus the presence or absence of hydathodes. All of the form species are considered to be simple, therefore "leaf organisation" is omitted. As indicated above Upchurch and Wolfe used only three leaf shape character states (the character FORM herein), only the first of which may be applied to the Clarence leaves, and even then, only to very few of them. Therefore, leaf form character states are given in greater detail (see Section 9.3).

Group 1 (OTUs 1,6,8,9,10,11,), plus OTU 14, corresponds to their mesophyllous unlobed Fig.4.1(f) (*Ficophyllum*) leaves, said to indicate evergreen plants in a humid moderate environment in the understory of a multistratal forest.

Group 2 (OTUs 5,7,12,13), plus OTU 4, corresponds to a variety of their foliar physiognomic types. OTUs 4,5 and 13 are somewhat similar to their Fig.4.1(a) (*Celastrophyllum obovatum*). OTU 7 is similar to their Fig.4.1(p) (*Liriodendropsis*) and OTU 12 might be considered similar to their Fig.4.1(d) (Drewrys Bluff Type No.1). Generally, these would indicate stenophyllous (except OTU 7), evergreen, stream-side plants.

Group 3 (OTUs 14,15,22) has no cohesion. OTU 14 has some similarity to their Fig.4.1(f) (*Ficophyllum*). OTU 15 has no counterpart in their types. OTU 22 approaches their Fig.4.1(q) (*Liriophyllum*).

Group 4 (OTUs 4,16,17,18,21) contains leaf forms similar to each other except for OTU 4 (see above). OTU 16 has no counterpart in their types. OTUs 17,18, and 21 may all be related to their

Fig.4.1(e) (*Rogersia*) type. This leaf type is indicative of stenophyllous stream-side plants in a dry area. The very membranaceous lamina and lack of hydathodes of these members (17,18,21) of the group suggest they were deciduous, but their entire margins suggest they were evergreen. It is possible they represent leaflets of compound leaves but no fossils have so far been found which would support this suggestion.

Group 5 (OTUs 2,3,19,20) approaches their Fig.4.1(m) ("*Viburnum*"), some being unlobed (OTUs 2,3), some being serrate or coarsely crenate (OTUs 3,19,20) and some having highly branched basal secondaries (OTUs 19,20). This leaf type is indicative of deciduous plants in a mesothermal successional or understory environment.

Summary

The 22 leaf form species established above (Section 9.4.1) are divided into groups by cluster analysis of particular characters which apparently have no intrinsic morphological or environmental basis. However, using the environmentally based characters of Upchurch and Wolfe (1987), the leaf form species described below may be ascribed to six leaf form genera *sensu* Spicer (1986), i.e. on the basis of shared architectural characters. It must be emphasised that while these leaf form genera are named from their morphotypes, their distinction from one another is established on the basis of as many characters as possible employing numerical taxonomic methods.

The gross morphologies of the form genera serve not only as the basis of their nomenclature, but also possibly indicate the environment in which they lived. However, a most striking feature of the Clarence series of fossil morphotypes is that they are, in general, very distinct from their Northern Hemisphere coeval counterparts. It follows also that even if the morphological/ecological correlation conjectures of Upchurch and Wolfe are broadly sound for North America, they may not hold true for the Clarence.

The OTUs discussed above are described in Section 9.5 under the following names:

- OTU 1 *Ficoidophyllum ellipticum*
- OTU 11 *F.attenuatum*
- OTU 9 *F.caperatum*
- OTU 10 *F.cuneatum*
- OTU 14 *F.oligodon*
- OTU 8 *F.ovatum*
- OTU 6 *F.recurvum*
- OTU 19 *Latifolium parvilobum*
- OTU 2 *L.acutum*
- OTU 20 *L.crenatum*
- OTU 3 *L.serratum*
- OTU 16 *Lauroidophyllum cryptocaroides*
- OTU 17 *L.cinnamomoides*
- OTU 22 *Liriophyllites parvisinus*
- OTU 13 *Parvifolium asymmetricum*
- OTU 4 *P.crenatum*
- OTU 7 *P.emarginatum*
- OTU 12 *P.membranaceum*
- OTU 5 *P.obovatum*
- OTU 15 *Proteaceophyllum irregulare*
- OTU 18 *P.lanceatum*
- OTU 21 *P.oblongum*

9.5. Systematic Description of Dicotyledonous Genera and Species

a. Leaves

The descriptive terms used are those of Hickey (1973) and Dilcher (1974) plus those defined in Sections 9.2 and 9.3 above. The order of characters given in the descriptions of species follows that given in Section 9.3 and Table 9.1. Measurements in **bold type** are from the holotypes: those in () brackets indicate ranges within the species. Specimen numbers are all from the Department of Plant and Microbial Sciences, Canterbury University collection (CU) from the middle Clarence valley (Cl) area. They represent block numbers, while # indicates a particular leaf as shown on plate overlays to Plates 5-9 in Volume 2. Other collection number prefixes used are:- B = New Zealand Geological Survey; zp = Canterbury Museum; c = Otago Museum.

The 22 leaf form species described are assigned to one of six form genera. These have been instituted because of character combinations which preclude reference of any of the species to existing genera (see Sections 1.6 and 9.4.2). Three of the genera, *Liriophyllites*, *Lauroidophyllum* and *Proteaceophyllum*, have certain characters which suggest tenuous phylogenetic relationships. The other three, *Ficoidophyllum*, *Latifolium* and *Parvifolium* are entirely morphologically derived. The last two are nomenclaturally invalid and must be renamed for formal publication.

The genera may be distinguished as follows:-

- | | |
|--|-------------------------|
| 1a. Tertiaries percurrent | <i>Latifolium</i> |
| b. Tertiaries reticulate | 2 |
| 2a. Apex bilobed, midrib divided at apex | <i>Liriophyllites</i> |
| b. Apex not bilobed, midrib ending in apex | 3 |
| 3a. Secondaries brochidodromous, basals more acute and
extending at least half way up lamina, base asymmetrical | <i>Lauroidophyllum</i> |
| b. Secondaries brochidodromous or semicraspedodromous,
basals not differentiated, base symmetrical | <i>Proteaceophyllum</i> |
| c. Not as above | 4 |
| 4a. Leaf notophyll to mesophyll, ovate to elliptic, apex acute to attenuate,
areoles imperfect or incomplete (except <i>F. oligodon</i> , well developed) | <i>Ficoidophyllum</i> |
| b. Leaf microphyll, form variable, apex variable,
areoles well developed | <i>Parvifolium</i> |

9.5.1. *Ficoidophyllum* gen.nov.

Type: *Ficoidophyllum ellipticum*.

Diagnosis: Leaf simple, petiolate, lanceolate to elliptic, notophyll to mesophyll; apex attenuate to acute; margin usually entire, sometimes irregularly crenate; lamina usually chartaceous, sometimes membranous; secondaries pinnate, craspedodromous or camptodromous, parallel; tertiaries random reticulate; areoles random, irregular, large to very large, lacking veinlets.

Derivation: from *Ficus* - the genus, *oid* - Greek, indicating resemblance, and *phyllum* - in Greek compound, relating to leaves.

Discussion: this genus is established as a form genus for accommodating mesophyllous, ovate to elliptic, unlobed, pinnately veined leaves similar to the leaf architectural group 7 of Hickey (1984) and the foliar physiognomic type "f" (*Ficophyllum*) of Upchurch and Wolfe (1987, Fig.4.1). Leaves ascribed to the new genus lack the brochidodromous secondaries and enclosing tertiary loops of *Ficophyllum crassinerve* Fontaine, illustrated by Hickey and Doyle (1977, Fig.11,13,16,60), although one of the new species (*Ficoidophyllum oligodon*) approaches this condition, being semicraspedodromous and having enclosing tertiary loops.

Crabtree (1987), in considering Northern Rocky Mountain (NRM) Albian to Campanian megafloras, instituted the morphotype "Magnoliaephyll" for simple ovate to elliptic leaves with entire or 2- or 3-lobed margin. They have brochidodromous or festooned brochidodromous secondaries. In this morphotype he placed (loc.cit.p.725) "a large number of problematic taxa that form an important part of all but extreme northern Laurasian floras. The group is erected primarily for convenience due to the enigmatic positions of most of its members. --- "*Magnolia*" *magnifica* Dawson is illustrated as an example of the morphotype." He included (loc.cit.p.716) "*Liriodendropsis* Newberry, *Liriophyllum* Lesquereux and *Magnoliaephyllum* (Krasser) Seward" in a list of important genera assigned to the morphotype. Their lack of brochidodromous secondaries precludes the inclusion of the Clarence fossils in this morphotype.

Of the genera described by Hickey (1977) from the Late Palaeocene/ Early Eocene of western North Dakota, all of *Acrovena*, *Averrhoites*, *Canariophyllum*, *Cornus*, *Dicotylophyllum*, *Kalmia*, *Paraternstroemia*, *Persites* and *Temstroemites* are ovate to elliptic leaves with pinnate venation. The major characters precluding their use for the Clarence fossils are:

Acrovena Hickey, a fossil genus in the Melastomataceae, has apex acuminate; venation perfect acrodromous; tertiaries forming a distinct V on either side of the midvein.

Averrhoites Hickey, a fossil genus tentatively assigned to the Oxalidaceae, has an odd number (as many as eleven) of alternate to opposite leaflets arranged pinnately, the leaflets being entire, asymmetrical, ovate to elliptic; apex acuminate; secondaries angle of divergence wide to moderate, brochidodromous or eucamptodromous; tertiaries transversely ramified to weakly percurrent; areolation equant and polygonal.

Canariophyllum Hickey, a fossil genus tentatively assigned to the Burseraceae, has apex abruptly acuminate; secondaries brochidodromous; tertiaries percurrent.

Cornus Linnaeus, a modern genus in the Cornaceae, has venation perfect acrodromous; tertiaries strongly percurrent.

Dicotylophyllum Saporta, a fossil genus of uncertain affinities, has margin dentate or serrate; tertiaries random or weakly percurrent; areolation equant and pentagonal or polygonal.

Kalmia Linnaeus, a modern genus in the Cornaceae, has apex acuminate; no glands; secondaries sinuous and irregular, often branching, mostly brochidodromous but occasionally eucamptodromous; areolation equant and pentagonal.

Paraternstroemia Hickey, a fossil genus in the Theaceae, has leaf texture smooth and coriaceous; venation brochidodromous; all veins but the primary immersed in the leaf substance; margin with closely spaced glandular serrulations.

Persites Hickey, a fossil genus in the Lauraceae, has apex obtuse, frequently emarginate, occasionally acute to slightly acuminate; venation camptodromous, mostly brochidodromous, rarely eucamptodromous, secondaries diverging at angles of 70° to 85° ; marginal ultimate venation looping; areolation mostly equant and quadrangular.

Temstroemites Berry emend. Hickey, a fossil genus in the Theaceae, has apex and base both acuminate; margin mildly crenate; secondaries ascending along the margin, mostly connected to the

superadjacent secondary by a series of percurrent tertiaries, though occasionally brochidodromous; areolation equant and polygonal. The emendation includes the presence of a glandular serrate margin. The glands are described (Hickey, 1977, p. 141, 145, Fig. 4, 6) as "thick marginal bristle[s]" and correspond closely to the structures herein termed hydathodes. Their occurrence in three of the species of *Ficoidophyllum* described here is associated with the secondary veins which end in irregular crenations.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. Some of the form species ascribed here to *Ficoidophyllum* show some characters in common with the Ettingshausen species. These are detailed below where appropriate.

Among the fossils described by Unger (1864) from Nelson Province are two leaves, now known only from the illustrations, which he ascribed to a new species *Phyllites nelsonianus*. The species is simply described (loc. cit. p. 11) as "*Ph. foliis ovatis acuminatis petiolatis integerrimis nervis secundariis distantibus simplicibus alternis.*" While this description accommodates both leaves, the illustrations (loc. cit. PL. 4, Figs. 7, 8) suggest that they differ in many characters. One of them, Fig. 7, is drawn as being symmetrical lanceolate with secondaries eucamptodromous, at an acute angle to the midrib, course straight, curvature uniform. It lacks apex and base. The other, Fig. 8, is drawn as being asymmetrical elliptic with secondaries eucamptodromous, at varying wide angles to the midrib, course sinuous, curvature abrupt. It has an asymmetrical, apparently normal base but lacks an apex. These leaves are closer to the Clarence *Ficoidophyllum* spp. than any described by Ettingshausen. Fig. 7 approaches *F. ovatum*. Fig. 8 has a character combination not present in the Clarence fossils but could be considered to approach both *F. recurvum* and *F. caperatum*. However neither is sufficiently similar to suggest any of the Clarence species should be included in *Phyllites nelsonianus*.

Ficoidophyllum is therefore established as a form genus without familial connotations. Seven species are recognised here from the Clarence flora. They are superficially similar to each other but may be distinguished by characteristic combinations of several characters. Individual leaves are commonly fragmentary but may be provisionally assigned to a species using the following characters (see Sections 9.2 and 9.3 for definitions):

Secondary Vein Curvature:

Straight on one side of midrib, recurved on other	<i>F.recurvum</i>
Uniform	<i>F.attenuatum, F.cuneatum</i>
Abrupt	<i>F.ellipticum, F.ovatum, F.caperatum, F.oligodon</i>

Secondary Vein Branching:

Unbranched	<i>F.ovatum</i>
Equal branching	<i>F.attenuatum, F.oligodon</i>
Lower branching	<i>F.ellipticum, F.caperatum, F.cuneatum, F.recurvum</i>

Base Angle:

Acute	<i>F.caperatum, F.cuneatum, F.recurvum</i>
Obtuse	<i>F.ellipticum, F.attenuatum, F.ovatum, F.caperatum, F.oligodon</i>

Basal Symmetry:

Symmetrical	<i>F.cuneatum</i>
Slightly asymmetrical	<i>F.attenuatum, F.caperatum, F.recurvum</i>
Asymmetrical	<i>F.ellipticum, F.ovatum, F.caperatum, F.oligodon</i>

Apex:

Attenuate	<i>F.attenuatum, F.ovatum, F.caperatum, F.cuneatum</i>
Acute	<i>F.ellipticum, F.recurvum, F.oligodon</i>

Intersecondary Veins:

Absent	<i>F.ellipticum, F.attenuatum, F.ovatum</i>
Simple	<i>F.cuneatum</i>
Composite	<i>F.caperatum, F.recurvum, F.oligodon</i>

Ficoidophyllum ellipticum sp.nov.

Holotype: CU 100.16#2 Cl.

Collection: Horse Flat, J.D.Lovis et al., April, 1979.

Diagnosis: leaf symmetrical, elliptic to narrow ovate, notophyll; apex acute; base asymmetrical, decurrent, obtuse; secondaries simple craspedodromous, branching lower, curvature abrupt.

Other material measured: Horse Flat 100.03#2,#4,#5, 100.04#10/100.05#8, 100.04#12/100.34#4, 100.04#13, 100.08#5,#19, 100.10#1, 100.14#2/100.17#14, 100.14#4/#8, 100.14#6/100.17#14a, 100.17#6,#13, 100.17#10/100.15(base), 100.19, 100.22#2,#3, 100.24#2, 100.25#4,#8, 100.27, 100.31.

East Quail Flat 310.22, 310.27.

Other material included: Horse Flat 100.06#1, 100.10#3, 100.14#1,#16?, 100.16#4,#5, 100.17#1,#3,#5, 100.20#5 (also on 100.14b and 100.15a), 100.22#1, 100.24#1, 100.25#5, 123.12#1.

Number of specimens included: 39 plus 1 uncertain.

Plate 28A.

Derivation: from *ellipticus*- Latin, meaning elliptic, referring to the leaf form.

Description: leaf simple, petiolate, symmetrical, elliptic to narrow ovate, notophyll, (5.5-) 8.5 (-14.5)cm. long, (2.5-) 3.4 (-4.6) cm. wide, L/W 2.2-3.2, L/BTOW 2.0-2.9; apex acute (28^0 -) 45^0 (-69^0); base asymmetrical, decurrent, obtuse (94^0 -) 119^0 (-139^0); margin entire with secondaries occasionally ending in a hydathode; lamina chartaceous.

Primary vein stout, straight to slightly sinuous. Secondaries pinnate, simple craspedodromous, angle of departure uniform, moderate acute (47^0 -) 57^0 (-65^0), moderately thick, branching lower, course sinuous, curvature abrupt, parallel, intersecondaries lacking. Tertiaries angle of origin acute exmedially, right angle admedially, random reticulate; highest order of venation observed third; areoles not observed.

Discussion: this species is selected as the type for the genus because it has a suite of characters which combines the various characters occurring in other species ascribed to the genus.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. The only Ettingshausen species which *F.ellipticum* approaches is *Ficus sub lanceolata* from Shag Point but it has brochidodromous secondaries departing at a wider angle than that of *F.ellipticum*. Also, the tertiaries of *F.sub lanceolata* are orthogonal reticulate. *Phyllites karamu* Hect. n.n. from Wangapeka is elliptic, entire and has craspedodromous secondaries with lower branches. Although illustrated (Hector 1886, Fig. 24A.2), the species was never described, and since the identity of the fossil which the drawing represents is unknown, it cannot be used as the basis for a valid species.

Ficoidophyllum attenuatum sp. nov.

Holotype: CU 100.17#2 Cl.

Collection: Horse Flat, J.D.Lovis et al., April, 1979.

Diagnosis: leaf symmetrical, narrow ovate to lanceolate, mesophyll; apex attenuate; base slightly asymmetrical, decurrent, obtuse; margin sometimes slightly crenate; secondaries cladodromous, thick, branching equal, curvature uniform; areoles imperfect.

Other material measured: Horse Flat 100.01#1, 100.03#6?, #11, #15, 100.05#2, #3, 100.08#2, #14, 100.10#2/100.09, 100.13#1, #2, 100.14#3/100.17#14b, 100.14#12, #13, #15/100.08, 100.23, 121.11; East Quail Flat 330.42#1.

Other material included: Horse Flat 100.16#1, 100.17#4?,#4a?,#12a?, 123.16; East Quail Flat 330.42#2.

Number of specimens included: 21 plus 4 uncertain.

Plate 28B.

Derivation: from *attenuatus* - Latin, meaning attenuate, referring to the apex.

Description: leaf simple, petiolate, symmetrical, narrow ovate to lanceolate, mesophyll (10.6-) 14.0 cm. long, (3.2-) 4.4 (-5.2) cm. wide, L/W 2.6 - 3.4, L/BTOW 2.1 -3.3; apex attenuate (21^0 -) 28^0 (-40^0); base slightly asymmetrical, decurrent, obtuse (70^0 -) 100^0 (-104^0); margin entire or slightly crenate, occasionally with hydathodes; lamina chartaceous; petiole length and width unknown.

Primary vein stout, straight or slightly curved. Secondaries pinnate, cladodromous, angle of departure uniform, moderate acute (44^0 -) 57^0 (-68^0), thick, branching equal, course sinuous, curvature uniform, parallel, intersecondaries lacking. Tertiaries angle of origin acute exmedially, right angle admedially, random reticulate; highest order of venation observed third, marginal ultimate venation incomplete; areoles imperfect, random, irregular, very large, lacking veinlets.

Discussion: this species is distinctive because it is a large leaf with a very attenuate apex, characteristically with straight sides at less than 40^0 but sometimes deformed (CU100.10#2Cl) or bent (CU100.02#1Cl). The secondaries are conspicuous, have a uniform curvature but a sinuous course, and are distinctively equally branched.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. Only *Myrica proxima* Ett. from Malvern Hills (now known only from Ettingshausen's illustration) has secondary vein characters similar to those of *F.attenuatum*, but it has a serrate margin. Also, the leaf is drawn as being incomplete, lacking both apex and base, thus in any case rendering equivocal any reference of these Clarence fossils to this taxon. The only Ettingshausen species with an apparently attenuate apex is *Cupanites novae zeelandiae* Ett. Ettingshausen (1891,p.306) describes it as "*versus angustatis*". Of the specimens in existence (zp 125-132), only zp 125 has an attenuate apex. However the secondaries are unbranched and the leaf form is asymmetrical so *F.attenuatum* cannot be referred to it.

Ficoidophyllum caperatum sp.nov.

Holotype: CU 100.03#7/100.34#3 Cl.

Collection: Horse Flat, J.D.Lovis et al., April, 1979.

Diagnosis: leaf asymmetrical, narrow elliptic to lanceolate, notophyll; apex attenuate; base slightly asymmetrical, decurrent, acute; lamina membranous, wrinkled; secondaries eucamptodromous to cladodromous, branching lower, curvature abrupt, weak basal pair more acute; areoles incompletely closed meshes.

Other material measured: Horse Flat 100.01#4/100.06, 100.05#5,#6, 100.07#12, 100.08#9,#13,#15,#16,#20, 100.14#14, 100.17b#12,#12b, 100.21#3, 100.25#1,#3, 100.26#1, 123.17; Ptilophyllum Ridge 522.62#2,#3,#9; Lower Seymour Stream 613.18, 613.22.

Other material included: Horse Flat 100.01#5, 100.06#3, 100.25#6; East Quail Flat 330.25?; Lower Seymour Stream 613.25?.

Number of specimens included: 27 plus 2 uncertain.

Plate 28E.

Derivation: from *caperatus* - Latin, meaning wrinkled, referring to the wrinkled lamina.

Description: leaf simple, petiolate, asymmetrical, narrow elliptic to lanceolate, notophyll, (3.8-) 10.0 cm. long, (2.0-) 3.3 (-4.8) cm. wide, L/W 2.4 - 3.3, L/BTOW 2.1 - 2.6; apex attenuate (33^0 -) 38^0 (- 57^0); base decurrent, acute to rarely obtuse (52^0 -) 84^0 (- 118^0), slightly asymmetrical when acute, very asymmetrical when obtuse; margin entire, hydathodes lacking; lamina membranous, wrinkled; petiole to 2.5 cm long, 0.1 cm wide.

Primary vein moderate, straight except when bent by ~~distortion~~. Secondaries pinnate, eucamptodromous to occasionally cladodromous, angle of departure uniform to irregular, moderate to wide acute (41^0 -) 60^0 (- 67^0) with weak basals more acute, fine, branching lower, course sinuous,

curvature abrupt, parallel, intersecondaries composite. Tertiaries angle of origin acute exmedially, obtuse admedially, random reticulate; highest order of venation observed third, marginal ultimate venation incomplete; areoles incompletely closed meshes, random, irregular, large, veinlets lacking.

Discussion: this species is distinguished from others in the form genus by its asymmetry, acute decurrent base, wrinkled lamina and weak, more acute basal secondaries. The latter cannot be likened to the basilaminar secondaries of the *Cinnamomum* type. Medial secondaries usually branch near the margin, both branches curving up but not reaching the margin. Small leaves with the same characters are interpreted as "juvenile" leaves.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. He described numerous species with narrow elliptic to lanceolate leaf forms with entire margins and camptodromous venation, but all have cuneate or normal bases and acute apices. *Diospiros novae-zeelandiae* Ett. (1887, Pl.5, Fig.4,4a, zp 86) has similar venation and leaf form but lacks the apex and almost all of one lateral margin. A comparison sufficiently comprehensive to establish common identity is therefore not possible.

Phyllites nelsonianus Unger PL.4, Fig.8 (see reference above) has similarly uniform to irregular, moderate to wide acute secondary vein angle and asymmetrical, narrow elliptic leaf form but its very asymmetrical base and lack of secondary branches preclude reference of the Clarence fossils to this taxon. *Magnolia magnifica* Dawson (as shown in Bell 1956, Pl.79, Fig.1) has similar leaf form but has brochidodromous venation.

Ficoidophyllum cuneatum sp.nov.

Holotype: CU 100.14#9 Cl.

Collection: Horse Flat, J.D.Lovis et al., April 1979.

Diagnosis: leaf symmetrical, lanceolate, notophyll, apex attenuate, base symmetrical, cuneate, wide acute; secondaries eucamptodromous to cladodromous, branching lower, curvature uniform, areoles imperfect.

Other material measured: Horse Flat 100.12#3, 100.13#3, 123.12#2; East Quail Flat 310.38; Ptilophyllum Ridge 522.62#1.

Number of specimens included: 6.

Plate 28D.

Derivation: from *cuneatus* - Latin, meaning cuneate, referring to the base.

Description: leaf simple, petiolate, symmetrical, lanceolate, notophyll (6.2-) 10.8 cm. long, (2.2-) 3.6 cm. wide, L/W 2.5 - 3.0, L/BTOW 1.8 -2.4; apex attenuate 32^0 (-45^0); base symmetrical, cuneate, wide acute (76^0 -) 86^0 ; margin entire, hydathodes if present inconspicuous; lamina chartaceous; petiole at least 1.3 cm. long, 0.1 cm. wide (on 100.12#3).

Primary vein moderate, straight. Secondaries pinnate, eucamptodromous to cladodromous,, angle of departure uniform, moderate to wide acute (52^0 -) 53^0 (-70^0), fine, branching lower, course sinuous, curvature uniform, parallel, intersecondaries simple. Tertiaries angle of origin right angle, random reticulate; highest order of venation observed third; areoles imperfect, random, irregular, large, veinlets lacking.

Discussion: this species is very like *F.attenuatum* but has a more acute, symmetrical, cuneate base, less distinctive secondaries and hydathodes are not evident. This species and *F.attenuatum* may belong to the same plant, whereon *F.cuneatum* is the terminal leaf, and *F.attenuatum* asymmetrical lateral leaves. It is separated from *F.caperatum* by its symmetrical lamina and base, secondaries which curve uniformly, lack of weak basal secondaries, and by not being wrinkled.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. Those with a symmetrical lanceolate leaf, cuneate base and camptodromous venation are *Apocynophyllum affine*, *Cassia pseudomemnonia*, *C.pseudophaseolites*, *Dalbergiophyllum rivulare*, *Diospiros novae-zeelandiae* and *Palaeocassia phaseolites*. None has the attenuate apex and fine venation characters of the Clarence fossils.

Ficoidophyllum oligodon sp.nov.

Holotype: CU 214.20 Cl.

Collection: Alexander McKay Terrace, I.L.Daniel and J.D.Lovis, Feb. 1986.

Diagnosis: leaf symmetrical, narrow ovate, mesophyll; apex rounded acute; base very asymmetrical, decurrent, obtuse; margin entire to coarsely crenate; secondaries semicraspedodromous, occasionally looping to join superadjacent secondary, thick, course irregular, curvature abrupt, branching equal, areoles well developed.

Other material included: Alexander McKay Terrace 129 specimens; East Quail Flat 330.06, 330.16, 330.18?; West Quail Flat 412.08, 412.11; Ptilophyllum Ridge 522.55, 522.57, 522.62#6,#7, 522.76; Upper Seymour Stream 742.40(3 specimens).

Number of specimens included: 142.

Plate 29A-C.

Derivation: from *oligo* - Greek, meaning few, and *odon* - Greek, meaning teeth.

Description: leaf simple, petiolate, symmetrical, narrow ovate, mesophyll (11.0-) 13.3 cm. long, (4.8-) 6.8 cm. wide, L/W 2.0 (-2.3), L/BTOW 2.4 (-2.75); apex rounded acute 30^0 ; base very asymmetrical, decurrent, obtuse 160^0 ; margin entire to coarsely crenate with occasional hydathodes; lamina chartaceous; petiole to 1.5 cm. long, 0.1cm wide.

Primary vein stout, straight below, sinuous above. Secondaries pinnate, semicraspedodromous, angle of departure uniform, wide acute 60^0 (-80^0), thick, often branching equally near margin, lower branch to margin ending in a hydathode, upper branch joining superadjacent secondary or becoming cladodromous, course sinuous to zigzag, curvature abrupt from branching points, parallel, loops if joining, at right angles, enclosed by tertiary loops, intersecondaries composite. Tertiaries obvious, angle

of origin right angle, random reticulate; highest order of venation observed fourth, thin, orthogonal, marginal ultimate venation incomplete; areoles well developed, random, irregular, large, veinlets lacking.

Discussion: this species is distinctively different from others in the form genus. Its secondaries are very irregular in type and course, and it has a characteristic asymmetrical base similar to that of *Trichilia hirta* Linnaeus (as shown in Hickey, 1977, Pl. 34, Fig. 2) or lateral leaves of *Tecomanthe speciosa* Oliver.

The only other extant member of the New Zealand flora with which this fossil has any features in common is *Heimerliodendron brunonianum* (Endl.) Skottsb. They are both large, narrow ovate leaves with slightly crenate margin, rounded acute apex, asymmetrical base and pinnate venation with equal branching. The latter however, has regular brochidodromous venation and lacks hydathodes. *F. oligodon* has a secondary vein pattern similar to that of *Wardiophyllum daturaefolium* (Ward) Hickey (1977, Pl. 53, Fig. 1) but its secondaries depart at a greater angle and reach the margin in slight crenations where they end in a hydathode, not „a "large, widely spaced, narrow, sharp-tipped dentation" (loc. cit. p. 150) as does the N. Dakota fossil.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species.

Ficoidophyllum ovatum sp. nov.

Holotype: CU 100.08#7 Cl.

Collection: Horse Flat, J.D. Lovis et al., 1979.

Diagnosis: leaf symmetrical, narrow ovate, notophyll; apex attenuate; base asymmetrical, decurrent, obtuse; secondaries eucamptodromous, unbranched, curvature abrupt; lamina chartaceous to sometimes membranous.

Other material measured: Horse Flat 100.01#6, 100.03#3, 100.03#9/100.05#7, 100.03#14/100.34#5, 100.07#3, 100.08#10,#17, 100.32.

Other material included: Horse Flat 100.08#11?,#18?, 100.17#7?.

Number of specimens included: 9 plus 3 uncertain.

Plate 28C.

Derivation: from *ovatus* - Latin, meaning ovate, referring to the leaf form.

Description: leaf simple, petiolate, symmetrical, narrow ovate, notophyll, (5.5-) 9.5 (-12.7)cm. long, (2.2-) 3.5 (-4.5) cm. wide, L/W 2.4 - 2.8, L/BTOW 2.4 - 3.0; apex attenuate 36^0 (- 43^0); base asymmetrical, decurrent, obtuse (83^0 -) 124 (- 150^0); margin entire, no hydathodes; lamina chartaceous to sometimes membranous; petiole at least 1 cm. long, 0.1 cm. wide, base not observed.

Primary vein stout, slightly sinuous. Secondaries pinnate, eucamptodromous, angle of departure uniform, moderate acute (46^0 -) 50^0 (- 60^0), fine, unbranched, course straight, curvature abrupt, parallel, intersecondaries lacking. Tertiaries not observed; areoles not observed.

Discussion: this species is distinguished from others in the form genus by its regular ovate form and unbranched secondaries. The apex is very similar to that of *F.attenuatum* and, if secondaries are not observable, apical fragments of the two taxa cannot be distinguished from each other.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. *Cassia pseudomemnonia*, *C.pseudophaseolites*, *Cupanites novae-zeelandiae*, *Dalbergiophyllum rivulare*, and *Palaeocassia phaseolitoides* all have ovate or lanceolate leaf form and camptodromous, unbranched secondaries, but all have an acute apex (except *C.novae-zeelandiae*, "*versus angustatis*", Ettingshausen, 1891,p.306), and normal acute base. Most are small leaves and none are described in sufficient detail to allow reference of these Clarence fossils to any of them.

One of the two leaves named *Phyllites nelsonianus* by Unger (1864), PL.4, Fig.7 (see reference above) is symmetrical, apparently ovate, with unbranched, uniformly curved secondaries, all of which correspond well with these Clarence fossils, but it lacks apex and base so complete comparison is not possible, and it is therefore unsafe to assume conspecificity.

Ficoidophyllum recurvum sp.nov.

Holotype: CU 522.73(2)#1 Cl.

Collection: Ptilophyllum Ridge, I.L.Daniel and J.D.Lovis, Feb. 1987.

Diagnosis: leaf asymmetrical, lanceolate, notophyll; apex acute; base slightly asymmetrical, cuneate, narrow acute; margin slightly crenate; secondaries simple, craspedodromous, angle of departure unequal laterally, thick, basal pair weak, more acute, branching lower, curvature straight on one side, recurved on other; areoles incompletely closed meshes.

Other material measured: East Quail Flat 330.43#1; Upper Seymour Stream 742.17, 742.21#1,#2.

Other material included: Horse Flat 100.25#9?; West Quail Flat 412.17?, 412.26?, 412.45?, Upper Seymour Stream 742.20?(4 fragments), 742.37?, 742.47?, 742.53?, 742.54?

Number of specimens included: 5 plus 12 uncertain.

Plate 28F.

Derivation: from recurvus - Latin, meaning recurved, referring to the secondaries.

Description: leaf simple, petiolate, asymmetrical, lanceolate, notophyll, 12.0 cm. long, (3.0-) 4.0 cm. wide, L/W 3.0, L/BTOW 2.4; apex acute 50^0 ; base slightly asymmetrical, cuneate, acute (47^0 -) 61^0 (-81^0); margin slightly crenate with hydathodes; lamina chartaceous; petiole to cm. long, cm wide .

Primary vein stout, curved. Secondaries pinnate, simple craspedodromous, angle of departure narrow acute, unequal laterally, one side (recurved) 36^0 (-61^0), the other side (straight) 50^0 (72^0), basal pair weak, more acute than upper secondaries and following margin, upper secondaries thick, branching lower, course sinuous, curvature straight or uniformly curved and recurved, parallel, intersecondaries composite. Tertiaries angle of origin right angle exmedially, acute admedially, random reticulate; highest order of venation observed third, marginal ultimate venation incomplete; areoles incompletely closed meshes, random, irregular, large, veinlets lacking.

Discussion: this species is distinguished from others in the form genus by its asymmetry of form and secondary vein angle, and the presence of a weak basal pair of secondaries at an angle more acute than that of the upper secondaries. The overall shape is similar to *Magnolia magnifica* Dawson and to *Ternstroemites aureavallis* Hickey but the venation is quite different, thus precluding reference of these Clarence fossils to either of these taxa.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. Species with asymmetrical, lanceolate leaf form and acute, cuneate base are *Apocynophyllum elegans*, *Cassia pseudophaseolites*, *Cupanites novae-zeelandiae*, *Sapindus subfalcifolius*, and *Laurophyllum tenuinerve*. None of these have recurved secondaries, so these Clarence fossils cannot be referred to any of these species. However, one of them, *A.elegans* from Landslip Hill, now known only from Ettingshausen's illustration (1887, PL.5, Fig.1), does have sinuous secondaries, at unequal angles on either side of the midrib, which appear to be craspedodromous. Ettingshausen (1891, p.276-277) however, describes the venation as "*camptodroma*" and the secondaries to be "connected with each other near the edge by anastomosing loops". Also (loc.cit) "the secondary nerves are fine and numerous, they are close together, winding, and start nearly at right angles from the primary nerve." The fossil was said to be housed in the Otago Museum (Ett.1891, p.277) but I have been unable to locate it.

Phyllites nelsonianus Ung. PL.4, Fig.8 (see reference above) has secondaries at unequal angles on either side of the midrib and the lower ones seem to recurve. However the base is very asymmetrical, the midrib is straight, and the secondaries lack branches so these Clarence fossils cannot be referred to it.

Latifolium gen.nov.

Type: *Latifolium parvilobum*.

Diagnosis: Leaf simple, petiolate, ovate, elliptic or oblong, notophyll or mesophyll, lamina very membranous, margin entire, lobed, coarsely crenate or sparsely serrate; secondaries pinnate, 4-6 pairs subopposite below, alternate above, simple craspedodromous, of approximately equal thickness, upper arcuate upwards, lower straight or curved downwards, parallel or diverging, usually ending in a hydathode, branching upper and/or lower or absent; tertiaries percurrent at a constant oblique angle to the midrib, alternate to subopposite about equal; areoles incompletely closed meshes, random, irregular.

Derivation: from *latus* - Latin, meaning broad, and *folium* - Latin, meaning leaf.

Discussion: this genus is established as a form genus for accom^modating broad, very membranous leaves with characteristic arcuate upper secondaries and percurrent tertiaries. The arcuate curvature of the upper secondaries is repeated by branches on the lower secondaries.

The 19 Ettingshausen, one Unger and one Laurent species of dicotyledonous fossil leaves described from New Zealand Cretaceous and Early Tertiary deposits, with which species of *Latifolium* have been compared, were assigned by the respective author to one or another of the following genera: *Alnus*, *Aralia*, *Artocarpidium*, *Cissophyllum*, *Dryophyllum*, *Fagus*, *Grewiopsis*, *Planera*, *Quercus*, *Ulmus* and *Ulmophylon*. All but *Artocarpidium*, *Cissophyllum*, *Dryophyllum*, *Grewiopsis* and *Ulmophylon* are excluded from consideration for use for the present fossils on the grounds that they are modern Northern Hemisphere genera (see Section 1.6).

Artocarpidium: Laurent (in Arber, 1917) assigned fossil dicotyledonous leaves from Upper Cretaceous deposits at Pakawau (see McQueen, 1955) to *Artocarpidium* Unger only after an exhaustive comparison of the vein architecture of the fossil with those of modern genera. He writes (loc.cit.p.63), "The authors who have adopted this genus have had especially in view the remains of the fructiferous receptacle: as for the foliar remains, they have been so little elucidated that they cannot be taken into

consideration. For our part, the term *Artocarpidium* recalls especially the relations of comparative nervation which we find between the New Zealand fossil and the group of modern Artocarpeae." Use of this genus for the Clarence fossils is precluded by the entire margin, opposite secondaries and reticulate tertiaries of *Artocarpidium*.

Cissophyllum: Ettingshausen (1891,p.282), in assigning a fossil from Tertiary deposits at Malvern Hills to the genus *Cissophyllum*, wrote "I rank this fossil leaf with the genera *Cissites* and *Ampelophyllum*" and placed it in the Ampelideae. He made no comparison of the new species he described, *Cissophyllum malvernium*, with species in other Tertiary floras or in the existing flora (loc.cit.p.246). The use of this genus for Clarence fossils is precluded by the firm and leathery texture, secondaries which "start with a somewhat diverging curve" (loc.cit.), and lack of preservation of tertiaries in the Malvern Hills fossil.

Dryophyllum: Ettingshausen assigned two species to the genus *Dryophyllum* which he placed in the Cupuliferae. The characters which persuaded Ettingshausen to assign these two species to the same genus elude me. Of one, *D.dubium* from Tertiary deposits at Landslip Hill, he writes (loc.cit.p.268) "the nervation (fig.19a) and the shape of the leaf indicate *Dryophyllum*". It is precisely the reticulate nervation and oblong shape which precludes equation of Clarence fossils assigned to *Latifolium* with this species. Of the other fossil, *D.nelsonicum* from Pakawau, he writes (loc.cit.p.298), "A fossil leaf which bears the type of *Dryophyllum*. The texture must be designated as firm and leathery; the edge is bluntly serrated; the secondary nerves which feed same are sharply defined and undivided, they are close to each other, little curved, not winding; the tertiary nerves are pronounced and run almost across". Since the *Dryophyllum* species from Sezanne and Dakota with which he compares the two New Zealand species respectively are unknown to me, I have been unable to obtain a clear impression of the characters defining the genus *Dryophyllum*. Therefore, I refrain from using it for Clarence fossils.

Grewiopsis: Ettingshausen assigned a fossil from Pakawau to *Grewiopsis* which he placed in the Tiliaceae. He wrote (loc.cit.p.305), "The fossil leaf described agrees best in its characteristics with *Grewiopsis*, and follows *G.orbiculata*, Sap., a species of the fossil flora of Sezanne which has small leathery leaves of a similar shape and nervation". The characters of size, texture, shape and venation stated by Ettingshausen to be characteristic of the genus all contribute to precluding assignment of Clarence fossils to *Grewiopsis*.

Ulmophylon: In the section devoted to fossils from deposits he placed in the Tertiary, Ettingshausen described two new species placed by him in the Ulmaceae. The specimens for one, *Ulmus hectori*, came from Shag Point, now known to be Late Cretaceous in age. He assigned it to *Ulmus* because (loc.cit.p.271) "in *Planera* it is unusual for the secondary nerves to start at acute angles, while this often occurs in *Ulmus*". The specimens for the second species, *Planera australis*, came from Shag Point, Malvern Hills and Murderer's Creek, the last two deposits indeed being Tertiary in age. He states (loc.cit.p.272) that *P.australis* shows "an extraordinary similarity with *Planera ungeri*,m., which is spread throughout the European Tertiary flora and the North American Tertiary strata". Later, in the section devoted to fossils from deposits he placed in the Late Cretaceous "Chalk Flora", he described a new genus, *Ulmophylon*, for some of the fossil leaves from deposits at Pakawau. He stated (loc.cit.p.300) "Among these I count fossil plants of the Chalk flora which according to their characteristics belong well to the *Ulmaceae*, but which cannot be enrolled with any living genus. The two species here described [*Ulmophylon latifolium* and *Ulmophylon planeraefolium*] have leathery leaves, one of which shows the closest relation to *Ulmus*, the other to *Planera*. Both genera are found in the Tertiary flora of New Zealand." Earlier, in the introductory section, he had stated (loc.cit.p.241) the Pakawau flora was characterised, in part, "by *Ulmophylon*, a genus comprising the ancestor-species of Tertiary *Ulmus*- and *Planera*-species". It is, therefore, clear that he intended the genus to be used for Cretaceous species of leaves which, when seen through European eyes, belonged in the Ulmaceae. However, he did not give a generic diagnosis, nor did he nominate a type species.

Oliver (1936,p.294) in discussing the assignment of a mid-Tertiary fossil he described as *Ulmophylon pliocenicum* to the genus stated "*Ulmophylon* was founded by Ettingshausen for two species from the Early Tertiary of New Zealand. The first species *U.latifolium* Ett., which may be selected as type of the genus, seems to be congeneric with the present species." Oliver not only placed *Ulmophylon* in the wrong period, but also apparently misunderstood Ettingshausen's intention that the genus represent an ancestral form. However, Ettingshausen's comparison of *U.latifolium* with *Ulmus prisca* Unger and *U.planeraefolium* with *Planera antiqua* Heer suggests that *U.latifolium* should indeed be regarded as the type species for *Ulmophylon*. Oliver (1950,p.10) later equated *Ulmophylon* with *Patete* Hector n.n. In view of the confusion surrounding *Patete scheffleri* and *Grewiopsis pakawauica* (see

Appendix 1), Oliver's equation of genera is best discounted, and the latter two genera left in isolation until further study of the fossils themselves elucidates their position.

In the absence of any clear statement of generic characters, apart from the leathery texture, Ettinghausen's concept of the genus *Ulmophylon* must be obtained from both *U.latifolium* and *U.planeraefolium*. *U.latifolium* (Syntypes zp 150, Ett.1887,PL.9,Figs.6,7 and zp 152; Ett.1887,PL.9, Fig.8 not found, see Gregg 1975) is the species with which the Clarence fossils assigned to *Latifolium* show most characters in common. It combines most of the salient features of *Latifolium crenatum* sp. nov. and *L.serratum* sp. nov., particularly the arcuate upper secondaries and lower branching. However, the lack of visible tertiaries in *U.latifolium*, and its finely crenate or serrate margin make it impossible to compare satisfactorily any of the present fossils with it. *U.planeraefolium* (Syntypes zp 149, Ett.1887,PL.9,Figs.2-5, and zp 151) is a small leaf with close-set, regular, straight secondaries and poorly percurrent tertiaries, all of which prevent comparison with it of any of the Clarence fossils except perhaps those assigned to *L.acutum* sp.nov. Even these are considerably larger, and have entire margins. If the only character explicitly indicated by Ettingshausen (lamina texture) is considered, none of the Clarence species can be placed in *Ulmophylon*. Thus, in spite of some similarities, it is considered inappropriate at this time to assign any of the Clarence species to that genus. Future investigations may allow its use, at least for some of the species.

Of the genera to which Hickey (1977) ascribed species described by him from the Late Palaeocene/Early Eocene of western North Dakota, all of *Ampelopsis*, *Betula*, *Corylus*, *Chaetoptelea*, *Dombya*, *Penosphyllum*, *Platanus* and *Protophyllum* are broadly ovate leaves with more or less arcuate upper secondaries and strong percurrent tertiaries. The major characters precluding their use for the Clarence fossils are:-

Ampelopsis Michaux, a modern genus in the Vitaceae, has a palmately-lobed, orbiculate leaf, perfect marginal actinodromous venation, cordate base, and cordate to obtuse teeth.

Betula Linnaeus, a modern genus in the Betulaceae, has about 10 pairs of secondaries and a doubly serrate, somewhat irregular margin.

Corylus Linnaeus, a modern genus in the Betulaceae, has 8-9 pairs of opposite to subopposite secondaries, and a margin doubly or triply cut into obtuse, apiculate dentations or serrations.

Chaetoptelea Liebmann, a modern genus in the Ulmaceae, has 12 pairs of irregularly placed secondaries, and a doubly (occasionally singly or triply) cut margin.

Dombeya Cavanilles, a modern, geographically restricted genus in the Sterculiaceae, has a palmately lobed, very wide ovate leaf, perfect marginal actinodromous venation with pectinals, deeply cordate base, and obtusely dentate margin.

Penosphyllum Hickey, a fossil genus placed in the Sterculiaceae, has an ovate leaf, pinnate camptodromous venation with pectinals, broadly to deeply cordate base, and entire margin.

Platanus Linnaeus, a modern genus in the Platanaceae, has a palmately lobed leaf, marginal palinactinodromous venation, obtuse to truncate base, and entire margin.

Protophyllum Lesquereux, a fossil genus placed in the Platanaceae, has an ovate leaf, 9 pairs of subopposite pinnate secondaries with pectinals, peltate base, and doubly dentate margin.

There is some similarity between *Latifolium* and the "protophyll" morphotype of Crabtree (1987, p.721) but the Clarence fossils do not have "basal secondaries sometimes strengthened considerably and bearing pectinals", or secondaries "brochidodromous if margin entire", or "orthogonal tertiaries".

Latifolium is therefore established as a form genus without familial connotations. Four species are recognised here from the Clarence flora. They may be distinguished by the following character combinations:-

L.parvilobum - ovate, secondaries diverging, lower curving down, branching upper and lower, base obtuse, margin lobed below, crenate above.

L.crenatum - elliptic, secondaries diverging, lower straight, branching lower only, base obtuse, margin crenate.

L.acutum - oblong, secondaries parallel, lower straight, branching lacking, base acute, margin entire.

L.serratum - elliptic, secondaries parallel, lower straight, branching lower only, base obtuse, margin entire below, serrate above.

Latifolium parvilobum sp.nov.

Holotype: CU 122.08 Cl.

Collection: Horse Flat, I.L.Daniel and J.D.Lovis, Jan. 1986.

Diagnosis: leaf ovate; base asymmetrical, decurrent, obtuse; margin lobed below, crenate above; secondaries angle of departure upper more acute, upper arcuate upward, lower curve down, diverging, branching upper and lower.

Other material included: Red Hill Stream, 5 specimens; Horse Flat, 32 specimens; Alexander McKay Terrace, 72+ specimens plus 7 uncertain; East Quail Flat, 16 specimens plus 6 uncertain; West Quail Flat, 40 specimens plus 9 uncertain; Ptilophyllum Ridge, 11 specimens plus 5 uncertain; Lower Seymour Stream, 4 specimens plus 3 uncertain; Upper Seymour Stream, 31+ specimens plus 20 uncertain; Coal Creek, 2 specimens.

Number of specimens included: 212 plus 54 uncertain.

Plates 31A, 32A-E.

Derivation: from *parvus* - Latin, meaning small and *lobus* - Latin, meaning a lobe.

Description: leaf simple, petiolate, symmetrical, ovate, mesophyll (4.3-) 14+ cm. long, (3.2-) 8+ (-10) cm. wide, L/W approximately 1.5, L/BTOW approximately 3.0 - 4.5; apex acute 40^0 (-53^0); base asymmetrical, decurrent, very obtuse (115^0 -) - (-200^0); margin lobed below crenate above, secondaries occasionally ending in a hydathode; lamina very membranous; petiole to 5 cm. long, 0.2 cm. wide with base slightly expanded to 0.3 cm.

Primary vein moderate, straight or slightly curved above. Secondaries pinnate, simple craspedodromous, angle of departure moderate acute (45^0 -) 48^0 (-65^0) upper more acute, alternate below subopposite above, moderately thick, branching lower and upper, course straight or occasionally sinuous, curvature of lower secondaries uniformly downwards or straight, of upper secondaries uniformly

arcuate upwards, of branches on lower secondaries the same as upper secondaries, diverging, intersecondaries lacking. Tertiaries angle of origin acute exmedially, right angle admedially, percurrent, forked, at a constant oblique angle to midrib, alternate and opposite about equally; highest order of venation observed fourth, relatively randomly oriented, marginal ultimate venation incomplete; areoles incompletely closed meshes, random, irregular, very large, veinlets branched once or twice.

Discussion: this leaf form is almost ubiquitous, occurring in all localities and in most horizons. It often occurs as closely overlapping "leaf beds" in locally derived sediments yet also occurs singly in transported sediments (crevasse splays, channel deposits and lacustrine beds). The expanded petiole base is not a pulvinus and together with the very membranous lamina, large size, non-entire margin and occurrence as leaf beds suggests the plant was seasonally deciduous.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. The more deeply lobed specimens resemble *Aralia tasmani* Ett. from Shag Point (transferred informally by Oliver, 1950 to *Acer*), but the surviving specimens (zp 90,91,92) show it to have basal actinodromous secondaries and orthogonal reticulate tertiaries. In contrast, the Clarence fossils assigned to *L. parvilobum* have basal secondaries narrower than the primary vein and of thickness equal to the medial secondaries which are alternate below, and percurrent tertiaries. *Cissophyllum malvernium* Ett. from Malvern Hills has outward curving basal secondaries with only lower branches, and has a slightly lobed margin. The sole existing specimen (zp 37) is a very poor impression not showing finer venation and is unsatisfactory as a basis for comparison.

Latifolium acutum sp.nov.

Holotype: CU 220.19 Cl.

Collection: Alexander McKay Terrace, I.L.Daniel and J.D.Lovis, Feb. 1986.

Diagnosis: leaf oblong; base asymmetrical, decurrent, acute; secondaries end in a hydathode, margin otherwise entire; secondaries angle of departure uniform, at less than 45^0 , upper arcuate upwards, lower straight, parallel, unbranched.

Other material included: Alexander McKay Terrace 214.14, 214.15, 217.08; East Quail Flat 330.21, 330.52; West Quail Flat 410.02?, 410.17?, 410.18?, 410.20?, 411.14, 411.19?, 411.24 (2 specimens), 411.25?, 411.28?, 411.30, 411.31, 411.32, 411.40, 412.15#2; Lower Seymour Stream 613.21, 613.25 (2 specimens plus 1 uncertain on back), 613.26; Upper Seymour Stream 718.01 (juvenile), 718.02, 718.03, 718.07, 718.07, 718.08, 718.10, 718.11?, 718.17?, 718.20 (base), 718.21 (apex), 718.23? (fragment), 718.56? (base).

Number of specimens included: 27 plus 13 uncertain.

Plate 31B.

Derivation: from *acutus* - Latin, meaning acute, referring to the basal angle.

Description: leaf simple, petiolate, symmetrical, oblong, notophyll (4.5-) 9.3 cm. long, (2.0-) 4.4 cm. wide, L/W 2.1, L/BTOW 1.86; apex acute to rounded 60^0 (-80^0); base asymmetrical, decurrent, acute (65^0 -) 76^0 ; margin entire, secondaries ending in a hydathode; lamina very membranous; petiole at least 2 cm. long.

Primary vein moderate, straight. Secondaries pinnate, simple craspedodromous, angle of departure uniform, narrow acute 43^0 , subopposite, thick, unbranched, course straight, curvature straight, uppermost slightly arcuate upwards, parallel, intersecondaries lacking. Tertiaries angle of origin acute exmedially, right angle admedially, percurrent, simple, convex, at a constant oblique angle to midrib, alternate and opposite about equally; highest order of venation observed fourth, thin, relatively randomly oriented, marginal ultimate venation incomplete; areoles incompletely closed meshes, random, irregular, large, veinlets simple, linear.

Discussion: this leaf form species is very similar to *L.crenatum* but differs in its oblong leaf form, narrower basal angle and, more particularly, the uniformly acute secondaries which are unbranched. It has uppermost secondaries with the curvature and arrangement characteristic of the form genus and very similar higher order venation, differing from *L.parvilobum* and *L.crenatum* only in having simple convex

tertiaries, and smaller areoles with simple linear veinlets. It could have been derived from *L.crenatum* by a regularization and simplification of the vein architecture.

Comparison with fossils described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand with similar vein patterns fails to reveal any closely comparable species. Eight of the Ettingshausen species have pinnate craspedodromous venation, uniformly acute, unbranched secondaries and percurrent tertiary (when visible). *L.acutum* is similar to *Quercus parkeri* Ett. from Shag Point (zp 64). This fossil is torn, not lobed as illustrated in Ettingshausen 1887, PL.3, Fig.23. However the Shag Point fossil lacks the characteristic arcuate upper secondaries of *Latifolium*, and has an obtuse base. Similarly *Quercus celastrifolia* Ett., also from Shag Point (zp 66), lacks the characteristic venation and has a serrate margin. *L.acutum* has venation very close to *Ulmophylon planeraefolium* Ett. from Pakawau (zp 150,152), but the latter is microphyllous and has a crenate margin and obtuse base. The remaining five species, *Dryophyllum nelsonicum* Ettingshausen (1887, PL.8, Figs.11,11a, not found, see Gregg 1975) from Pakawau, *Fagus nelsonica* Ett. (zp 98) and *Quercus nelsonica* Ett. (zp 97) from Wangapeka, *Fagus ulmifolia* Ett. from Shag Point (zp 49,68-71) and Wangapeka (zp 99) (informally referred to *Nothofagus* by Oliver 1950) and *Fagus ninnisiana* Unger (1864, PL.3, Figs.1-9) from Drury and Shag Point (c 48.27) (also informally referred to *Nothofagus* by Oliver 1950) all have serrate margins.

Block C48.27 from Otago Museum has broken and distorted leaves labelled "*Fagus ninnisiana* Ung". The back of this block, which is labelled only "Geological Survey of Otago No. FC ix Shag Point", nevertheless has some good leaves very like *L. acutum*. Block C48.62 also bears a leaf (also unidentified) very like *L.acutum*.

Artocarpidium arberi Laurent ex Arber (1917) from Pakawau (see McQueen, 1955) is an ovate, entire margined leaf with straight, parallel secondaries at an acute angle to the midrib, but it has a symmetrical, obtuse, normal base and reticulate tertiary.

Latifolium crenatum sp.nov.

Holotype: CU 220.12(2) Cl.

Collection: Alexander McKay Terrace, I.L.Daniel and J.D.Lovis, Feb., 1986.

Diagnosis: leaf elliptic; base asymmetrical, cuneate, obtuse; margin crenate; secondaries angle of departure uniform, upper arcuate, upwards lower straight to slightly curved upward, diverging, branching lower only.

Other material included: Alexander McKay Terrace 214.09, 220.09, 220.11 (1 large specimen plus one apical fragment), 220.12 (apical fragment); East Quail Flat 330.14 (4 specimens), 330.19?, 330.34, 330.36, 330.42(2); Ptilophyllum Ridge 521.10 (4 specimens plus 2 on back of b), 521.11 (several overlapping), 521.12 (several overlapping), 521.13, 521.14, 522 (several blocks) 30 specimens; Lower Seymour Stream 613 (several blocks) 25 specimens ; Upper Seymour Stream 750.01 (2 specimens), 750.02.

Number of specimens included: 77 plus 2 uncertain.

Plate 31C.

Derivation: from *crenatus*- Latin, meaning scalloped, referring to the margin.

Description: leaf simple, petiolate, symmetrical, elliptic, notophyll 12.2 cm. long, 6.2 cm. wide, L/W 2.0, L/BTOW 2.3; apex acute 35^0 ; base slightly asymmetrical, cuneate, obtuse 95^0 ; margin broadly crenate, secondaries ending in a hydathode; lamina very membranous; petiole to 5 cm. long, 0.2 cm. wide .

Primary vein moderate, straight. Secondaries pinnate, simple craspedodromous, angle of departure uniform, moderate acute 55^0 , subopposite, thick, branching lower, course straight, curvature of lower secondaries straight, of upper secondaries uniform arcuate upwards, diverging, intersecondaries lacking. Tertiaries angle of origin acute exmedially, right angle admedially, percurrent, forked, at a constant oblique angle to midrib, alternate and opposite about equally; highest order of venation observed fourth, thin, relatively randomly oriented, marginal ultimate venation incomplete; areoles incompletely closed meshes, random, irregular, very large, veinlets branched once or twice.

Discussion: this leaf form species is very similar to *L. parvilobum* but differs in being elliptic instead of ovate, has a cuneate, less obtuse base and lacks downward curving lower secondaries. Some specimens have some characters with states intermediate between the two species. Apical fragments cannot be distinguished to species. Comparison of the two suites of specimens shows that it is possible *L.crenatum* was derived from *L.parvilobum* by reduction of the basal part of the leaf.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. *L.crenatum* has a somewhat similar leaf form and venation pattern to *Ulmophylon latifolium* Ett. from Pakawau but lacks the serrate margin of the latter. Furthermore, the existing specimens of *U.latifolium*, (zp 150,152) lack discernable tertiaries. Ettingshausen's figure (Ett.1887,Pl.3,Fig.25) of *Quercus deleta* Ett. from Shag Point shows a leaf with a crenate margin, upward curving secondaries and apparently percurrent tertiaries. However, the secondaries differ from those of *L.crenatum*, being alternate and unbranched. Although the illustrated fossil has not been located (Gregg, 1975), a syntype, zp.65, is available. It confirms that the tertiaries are percurrent but differ from those of *L.crenatum* in having their angle of origin obtuse admedially, and in being recurved and predominantly alternate.

Latifolium serratum sp.nov.

Holotype: CU 121.01#1 Cl.

Collection: Horse Flat, I.L.Daniel and J.D.Lovis, Feb. 1985.

Diagnosis: leaf elliptic; base slightly asymmetrical, decurrent, obtuse; margin upper two thirds serrate, lower third entire; secondaries angle of departure increases upwards, curvature increases upwards, upper arcuate, parallel, branching lower, secondaries and branches end in acute serrate tooth.

Other material included: Horse Flat 121.01#2,#3, 121.09. Number of specimens included: 4.

Plate 31D.

Derivation: from *serratus*- Latin, meaning saw-edged, referring to the margin.

Description: leaf simple, petiolate, symmetrical, elliptic, notophyll (7.2-) 8.8 cm. long, (3.5-) 4.5 cm. wide, L/W 1.95, L/BTOW 1.95; apex acute 95^0 ; base slightly asymmetrical, decurrent, obtuse 110^0 ; margin entire below, serrate on upper two thirds, teeth acute, apical side straight, basal side convex, simple, sinus rounded, spacing irregular, ending in a hydathode; lamina very membranous; petiole terete, at least 2 cm. long, 0.1 cm. wide, base probably expanded.

Primary vein moderate, straight. Secondaries pinnate, simple craspedodromous, angle of departure narrow acute 44^0 , upper more obtuse, alternate below, subopposite above, moderately thick, branching lower, course straight to sinuous, curvature uniform arcuate, parallel, intersecondaries lacking. Tertiaries angle of origin variable, acute to right angles exmedially and admedially, percurrent, simple, convex, at a constant oblique angle to midrib, alternate and opposite about equally; highest order of venation observed fourth, thick, orthogonal, marginal ultimate venation looped; areoles incompletely closed meshes, random, irregular, medium, lacking veinlets.

species

Discussion: this leaf form_x is very similar to *L.crenatum* but differs in its elliptic leaf form, and in having a distinctly serrate upper margin, parallel secondaries, simple convex tertiaries and smaller areoles lacking veinlets. It has upper secondaries with the curvature and arrangement characteristic of the form genus and could have been derived from *P. crenatum* by regularization of the vein architecture and accentuated dentation of the margin. It fits the description by Hickey (1984, p.293) of his "leaf architectural type 8" (simple, pinnately veined leaves with toothed margins and craspedodromous secondary veins), a type not reported by Hickey and Doyle (1977) but possibly represented by the "foliar physiognomic type d (Drewrys Bluff leaf type No.1)" of Upchurch and Wolfe (1987).

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. Fifteen of the Ettingshausen species have pinnate, simple craspedodromous venation with parallel secondaries, percurrent tertiaries (where visible) and a more or less serrate margin. (Another, *Dryophyllum dubium* Ett. (c 48.58,59), agrees in all these characters except the tertiaries which are orthogonal reticulate.) Of these, *Dryophyllum nelsonicum* Ett. (not found, see Gregg, 1975), *Fagus nelsonica* Ett. (zp98), *F.ninnisiana* Ung (c 48.27), *F.lendenfeldi* Ett. (zp 33,34), *F.ulmifolia* Ett. (zp 49,68-

71,99)(the last two informally referred to *Nothofagus* by Oliver 1950), *Planera australis* Ett. (zp 35,36,74)(referred to *Zelkova* by Nagalhard, 1922), *Quercus celastriifolia* Ett. (zp 66), *Q.lonchitoides* Ett. (zp 1-4,23-25,32,67; c 48.35,37,41,66, see Gregg 1975, but the first three from Otago Museum not found), *Q.nelsonica* Ett. (zp97), *Ulmophyllum planeraefolium* Ett. (zp 149,151) and *Ulmus hectori* Ett. (c 48.29) lack lower branches, do not show arcuate upper secondaries and are ovate or oblong. *Grewiopsis pakawauica* Ettingshausen (1887,PL.9,Fig21, not found, see Gregg 1975)(informally referred to *Patete scheffleri* Hect. n.n. by Oliver, 1950) and *Fagus producta* Ett. (zp 167)(said by McQueen, 1955 to resemble *Artocarpidium arberi* Laurent ex Arber 1917) have few, minor lower branches, are finely serrate over most of the margin and show only slight upward curvature of the upper secondaries. *Ulmophylon latifolium* Ett. (zp 150,152) has upward curving secondaries with lower branches, but has a finely crenate or serrate margin with obtuse teeth, and is broadly ovate. Furthermore, the tertiary vein pattern is not sufficiently clear to allow comparison.

The species which *L. serratum* most closely resembles in leaf form and both secondary and tertiary vein pattern is *Alnus novae-zeelandiae* Ett. from Shag Point (zp 61-63, c 48.34) and Redcliffe Gully (not found, see Gregg 1975). However, *A.novae-zeelandiae* has a normal base, lacks prominent lower branches on the secondaries, and has obtuse teeth which are less well developed and more irregular than those in *L.serratum*, and have concave apical sides and straight basal sides. All specimens lack an apex.

Lauroidophyllum gen.nov.

Type: *Lauroidophyllum cryptocaroides*.

Diagnosis: Leaf simple, petiolate, symmetrical, narrow ovate to narrow oblong, microphyll; secondaries brochidodromous, basals more acute and extending at least half way up lamina, enclosed by tertiary loops.

Derivation: from *Laurus* the genus, from the Greek *Daphne*, and *oides* - Greek, indicating resemblance.

Discussion: Dilcher (1974,p.33) defined the term acrodromous as "two or more primary or strongly developed secondary veins running in convergent arches toward the leaf apex. Arches not recurved at base".

Samylin (1968,p.207), in describing *Cinnamomoides ievlevii*, included in the diagnosis "Venation, trinerved; midrib, straight reaching well into the apical region. Lateral primaries, opposite, inserted above the base, - - - curving upwards and running two-thirds to three-quarters the length of the leaf." i.e. acrodromous, basal, perfect in the terminology of Dilcher and implying three primary veins. Furthermore, she states (loc.cit.p.209) "The genus *Cinnamomoides* was established by Seward (1925) for leaves whose venation resembled that of *Cinnamomum* leaves, in particular *C.camphora*. - - - In most living species of *Cinnamomum* lateral primaries are given off higher than in those of *Cinnamomoides*."

Crabtree (1987) ascribed simple leaves with entire margins, pinnate venation with prominent suprabasal secondary veins arching apically, and transverse tertiary veins to a leaf morphotype "Cinnamomophyll". Both species described here under *Lauroidophyllum* gen.nov. could be included in his morphotype if it were not for their tertiary veins which are not transverse.

Krassilov (1977) states that "Cretaceous laurophylls with pinnate venation are placed in *Laurophyllum*, *Magnoliaephyllum*" etc. while those "with acrodromous venation are described as *Cinnamomoides*, *Lauraceaephyllum*, *Araliopsoides*, *Aralieaephyllum*, "*Sassafras*" and "*Benzoin*". Furthermore, he states "the laurophylls are rather uniform in their cuticular characters which constitute

major evidence of their attribution to the Laurales." In the absence of cuticular information for the Clarence fossils it is considered inadvisable to use any of the genera listed by Krassilov.

Holden (1982) discussed the constituents of the Family Lauraceae presently found in New Zealand, and fossils previously ascribed to that family. She described six new species from the Mid - Upper Miocene Longford Formation, ascribing one to *Cryptocarya*, three to ?*Cryptocarya*, one to ?*Cinnamomum* and one to ?*Litsea*. All have percurrent tertiaries. Differences between the Clarence and Longford species are detailed below.

The Clarence fossils, while presenting clearly "*Cinnamomum* -type" venation patterns, have basal secondaries half the width of the primary vein and of the same strength as the upper secondaries. Furthermore, the basal secondaries do not run "in convergent arches", but join with superadjacent secondaries to form brochidodromous loops approximately half way up the leaf. In both species here described, the tertiary vein pattern is reticulate. While the gross venation pattern suggests affiliation with genera ascribed to the Lauraceae, the absence of agreement of finer architectural features precludes attribution to any one of these genera. Therefore the form genus *Lauroidophyllum* is established to accommodate fossil leaves showing features of general resemblance to lauraceous genera. Two species are recognised here from the Clarence flora. One, *L.cryptocaroides*, has a pair of strong basal secondaries not parallel to the margin. The other, *L.cinnamomoides*, has a pair of weak basal secondaries which are parallel to the margin.

Lauroidophyllum cryptocaroides sp. nov.

Holotype: CU 212.01 Cl.

Collection: Alexander McKay Terrace, I.L.Daniel and J.D.Lovis, Feb. 1985.

Diagnosis: leaf narrow ovate, very membranous; secondaries brochidodromous, basal pair very strong, not parallel to margin, upper secondaries start one-third up leaf, exmedial tertiaries loop to join superadjacent tertiary.

Other material included: Horse Flat 100.01#1a; Alexander McKay Terrace 212.01 (4 fragments in addition to holotype) 214.21 (1 large specimen, 2 fragments), 217.08, 217.16; East Quail Flat 330.32; Lower Seymour Stream 613.17; Upper Seymour Stream 700.15 (2 specimens), 711.08 (1 specimen overlapping 3 fragments), 712.37 (4 specimens), 732.04?, 732.07?.

Number of specimens included: 25 plus 4 uncertain.

Plate 30A-D.

Derivation: from *Cryptocarya*, the genus, and *oides* - Greek, indicating resemblance.

Description: leaf simple, petiolate, symmetrical, narrow ovate, microphyll, (5,6-) 6.2 (-7.0)cm. long, (2.2-) 3.7 cm. wide, L/W 1.7, L/BTOW 2.7; apex acute (30^0 -) 36^0 (-37^0); base slightly to very asymmetrical, decurrent, wide acute to obtuse (83^0 -) 174^0 ; margin entire; lamina very membranous; petiole at least 1 cm. long, 0.2 cm. wide .

Primary vein stout, straight. Secondaries pinnate, brochidodromous, angle of departure moderate acute 75^0 , lowest pair more acute (32 - 46^0), thick, not parallel to margin, extending to half way up leaf, other secondaries of equal thickness, from one third way up leaf mostly alternate, branching lower, course straight, curvature uniform, joining superadjacent secondary at right angle, converging, enclosed by tertiary loops, intersecondaries lacking. Tertiaries angle of origin acute exmedially, right angle admedially, orthogonal reticulate; highest order of venation observed fourth, marginal ultimate venation looped; areoles well developed, oriented, quadrangular, very large, veinlets simple curved.

Discussion: the fossil is somewhat similar in general vein pattern to the Miocene *Cryptocarya longfordensis* Holden but differs in being not acrodromous, with basal secondaries not extending two thirds to three quarters up the leaf, in lacking intersecondaries and with tertiaries not percurrent. The Clarence fossils are also larger (6 x 4 cm compared with 4 x 2 cm.). Furthermore, *L.cryptocaroides* is separated in time from *C.longfordensis* by some 50 million years. In any case, it cannot be reliably assigned to the genus *Cryptocarya* without confirmation of cuticle structure.

The general vein pattern approaches that of *Cinnamomoides ovalis* (Dawson) Bell (1956) but the basal secondaries arise close to the base (cf. Bell, 1956, p.131, "generally well above the base") and

the "branches" (tertiaries) from them form loops rather than uniting "close to margin to form an apparent marginal vein"(loc.cit.).

Comparison with fossils described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species.

Lauroidophyllum cinnamomoides sp. nov.

Holotype: CU 522.62#4 Cl.

Collection: Ptilophyllum Ridge, I.L.Daniel and J.D.Lovis, Feb. 1987.

Diagnosis: leaf narrow elliptic, basal secondary pair weak, to half way up leaf, parallel to margin, joined by recurved secondaries, upper secondaries from half way up leaf loop to join superadjacent secondaries.

Other material included: Horse Flat 123.12#3; East Quail Flat 330.33.

Number of specimens included: 3.

Plate 30E&F.

Derivation: from *Cinnamomum*, the genus, and *oides* - Greek, indicating resemblance.

Description: leaf simple, petiolate, symmetrical, narrow oblong, microphyll, 5.0 cm. long, 1.7 (-2.4) cm. wide; apex acute (36^0); base very asymmetrical, cuneate, acute (45^0); margin entire; lamina very membranous; petiole to $1\frac{3}{4}$ cm. long, 0.1 cm. wide.

Primary vein moderate, straight to slightly curved. Secondaries pinnate, brochidodromous; basal pair more acute than upper secondaries, moderately thick, extending to half way up leaf parallel to margin, in lower half joined at right angles by fine recurved secondaries; secondaries from half way up leaf moderately thick, angle of departure moderate acute (57^0 -) 69^0 , loop to join superadjacent secondaries at right angles, branching lower, course straight, curvature uniform, converging, enclosed by tertiary loops, intersecondaries lacking. Tertiaries angle of origin right angle exmedially, acute

admedially, random reticulate, highest order of venation observed third; areoles incompletely closed meshes, random, irregular, very large, veinlets lacking.

Discussion: None of the specimens is complete. The Ptilophyllum Ridge specimen, although lacking both apex and base, is chosen as the holotype because it displays the contrasting secondary venation patterns of the lower and upper portions of the leaf. The Horse Flat specimen consists of the apical portion of the leaf only. Furthermore, the apex has been exposed by differential fracture. The result is that, because of the very membranaceous texture of the leaf, the venation is poorly presented. The East Quail Flat specimen consists only of the basal portion of the leaf. Furthermore, it has a very asymmetrical base which may or may not be typical of the species. In spite of their fragmentary nature, there is no doubt that 1) the three specimens are unique in the Clarence flora and 2) they should be placed in the same taxon.

The venation of these leaves is reminiscent of "*Cinnamomum*" *hesperidium* Knowlton (e.g. as shown in Crabtree 1987, Fig. 42). The Clarence fossils differ from ?*Cinnamomum miocenium* Holden which lacks well defined upper secondaries, has percurrent tertiaries, and has small, perfect, oriented areoles.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. Both *Cinnamomum intermedium* Ett., from Shag Point (zp 76-83) and Redcliffe Gully (zp. 27), and *C. haastii* Ett., from Pakawau (zp 136), have suprabasal acrodromous venation, lack brochidodromous secondaries, and have percurrent tertiaries.

9.5.4. *Liriophyllites* gen.nov.

Type: *Liriophyllites parvisinus*.

Diagnosis: Leaf simple, petiolate, bilobed, apex of each lobe rounded; venation pinnate, primary extending to base of sinus and forking into more or less prominent veins distinct from secondary veins below.

Derivation: from *Liriophyllum*, the Lesquereux genus emended by Dilcher and Crane 1984, and *ites* - Greek substantive suffix, indicating close connection.

Discussion: the emended diagnosis of *Liriophyllum* Lesq.(1878) by Dilcher and Crane (1984) states that the lamina is "deeply divided for at least half its length". The sinus of *L.parvisinus* extends for one fifth of the lamina length; therefore it cannot be included in *Liriophyllum*. The present collection includes only two specimens attributable to the new species thus giving insufficient evidence on which to judge whether further emendation of *Liriophyllum* so as to include the Clarence fossils is appropriate. Therefore a new genus is established to accommodate any bilobed leaf with a forking primary vein, regardless of sinus depth or behaviour of the primary vein after forking.

Dilcher and Crane (1984,p.369) excluded *Liriophyllum obcordatum* Lesquereux (1883) of Cretaceous age from the genus *Liriophyllum* because "it does not show these diagnostic features, particularly the bifurcation of the midrib". Dilcher and Crane (loc.cit.) also excluded *Liriophyllum sachalinense* Kryshtofovich (1937), also of Cretaceous age, from the genus *Liriophyllum* stating it "subsequently has been referred to *Bauhinia* by Vakhrameev (1966), Takhtajan (1974), and Tanai (1979)." Both species have an emarginate apex with a sharply V-shaped sinus base which is quite unlike that of both *Liriophyllum* and the present fossils.

Hickey (1984, p.294) states that his leaf architectural group 13 "the so-called genus *Bauhinia* with its unusual, deeply emarginate shape has been identified in Early Palaeocene sediments (Brown, 1962) although its relationship to the Cenomanian to Santonian "*Bauhinia*" line is not definitely established." Again, the present fossils have a very different sinus base shape from Hickey's leaf architectural group 13 and cannot be associated with it.

Liriophyllites parvisinus sp.nov.

Holotype: CU 214.19#2 Cl.

Collection: Alexander McKay Terrace, I.L.Daniel and J.D.Lovis, Feb. 1986.

Diagnosis: leaf bilobed, very wide obovate; apex emarginate; base symmetrical, decurrent, acute; secondaries and tertiaries prominent, looped, forming polygonal meshes.

Other material included: Alexander McKay Terrace 220.14a (distal half only).

Number of specimens included: 2.

Plate 29D&E.

Derivation: from *parvus* - Latin, meaning small, and *sinus* - Latin, meaning a rounded inward curve between two projecting lobes, referring to the apical part of the leaf and comparing it with *Liriophyllum populoides*.

Description: leaf simple, petiolate, symmetrical, very wide obovate, microphyll 4.5 cm. long, 4.8 cm. wide, L/W 0.91, L/BTOW 1.28; apex bilobed sinus extending for one fifth of length of lamina, apex of each lobe rounded, emarginate 323^0 ; base symmetrical, decurrent, acute 85^0 ; margin entire with occasional hydathodes; lamina membranous; petiole 1cm. long, 0.1 cm. wide with slightly swollen base.

Primary vein moderate, extending to base of sinus and forking into more or less prominent veins distinct from secondaries below and arching into lamina, straight below, more or less zigzag between secondaries above. Secondaries pinnate, eucamptodromous, branches occasionally joining superadjacent secondaries forming polygonal meshes, angle of departure more obtuse above and below, medial secondaries wide acute 67^0 , very obvious, sharply defined, thick, branching equal, course zigzag between points of branching, recurved, branches joining superadjacent secondaries at right angles, parallel, enclosed by tertiary vein loops, intersecondaries composite. Tertiaries obvious, angle of origin right

angle, random reticulate; highest order of venation observed fourth, marginal ultimate venation incomplete; areoles well developed, random, polygonal, large, veinlets branch twice.

Discussion: this leaf form is unique in the Clarence flora, only *Parvifolium emarginatum* sp.nov. (described below) approaching it in form and venation. It is also unique in being the only dicotyledonous species from the Clarence flora to show any similarity to a species from the coeval Dakota flora (pers.comm. David Dilcher, Nov.1988).

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species.

Parvifolium gen.nov.

Type: *Parvifolium asymmetricum*.

Diagnosis: Leaf simple, petiolate, microphyll; secondaries pinnate, parallel, branching equal or lower; tertiaries random or orthogonal reticulate; areoles well developed, random, irregular or polygonal, medium to large, veinlets lacking.

Derivation: from *parvus* - Latin, meaning small, and *folium* - Latin, meaning leaf.

Discussion: this genus is established as a form genus for accom^{ma}modating microphyllous leaves which do not fit in any of the other form genera described here and which also cannot reasonably be accom^{ma}modated in any genera described elsewhere. Five species are recognised here from the Clarence flora. Each species is distinct, being easily separated from all others on one or a few characters, especially leaf form and margin. *Parvifolium asymmetricum* is selected as the type only because it is probably the least likely to be able to be assigned to another genus! When additional specimens showing diagnostic characters are collected, some species included here may be transferred to other genera. In particular, *Parvifolium emarginatum* possibly belongs in *Liriophyllites*. The five species may be distinguished by the following character combinations:

P.asymmetricum:

leaf asymmetrical, elliptic; apex asymmetrical; base
asymmetrical acute; margin entire.

P.crenatum:

leaf symmetrical, elliptic; margin compoundly serrate
with rounded teeth; secondaries very thick and
uniformly curved, with upper and lower secondaries
more obtuse than medial secondaries;

lamina very membranous.

P.emarginatum:

leaf asymmetrical, wide elliptic; apex emarginate;
base asymmetrical, decurrent, obtuse; margin entire.

P.membranaceum:

leaf narrow ovate; apex acute; base asymmetrical,
decurrent, obtuse; margin irregularly crenate or wavy;
lamina very membranous.

P.obovatum:

leaf asymmetrical, narrow obovate; apex wide acute;
base symmetrical, cuneate, acute;
margin entire with occasional teeth.

Parvifolium asymmetricum sp.nov.

Holotype: CU 212.08(1)#3 Cl.

Collection: Alexander McKay Terrace, I.L.Daniel and J.D.Lovis, Feb. 1985.

Diagnosis: leaf asymmetrical elliptic, apex asymmetrical obtuse rarely acute, base asymmetrical, decurrent acute rarely obtuse, margin entire to slightly crenate, lamina chartaceous.

Other material included: Horse Flat 100.12#4/100.20#1, 123.11; Alexander McKay Terrace 212.08#5,#7?,#12?,#19?, 214.08 (base only), 214.19; East Quail Flat 300.17(on back), 310.37; Ptilophyllum Ridge 522.74#1,#2, 522.76#7; Lower Seymour Stream 613.15.

Number of specimens included: 12 plus 3 uncertain.

Plate 33A.

Derivation: from *asymmetricus* - Latin, meaning asymmetrical, referring to lamina, apex and base.

Description: leaf simple, petiolate, asymmetrical, elliptic, microphyll, 3.1 (-6.6)cm. long, (1.0-) 1.5 (-2.7) cm. wide, L/W 2.1 (-2.4), L/BTOW 1.8 (-2.7); apex asymmetrical, obtuse to rarely acute (63^0 -) 118^0 ; base asymmetrical, decurrent, acute to rarely obtuse (64^0 -) 82^0 (- 110^0); margin entire to slightly crenate; lamina chartaceous; petiole up to 1.3 cm. long, 0.15 cm. wide, commonly bent or curved.

Primary vein stout, straight. Secondaries pinnate, cladodromous, angle of departure irregular, moderate acute (49^0 -) 52^0 (- 77^0), moderately thick, branching equal, course sinuous, curvature straight, parallel, intersecondaries lacking. Tertiaries angle of origin right angle, random reticulate; highest order of venation observed fourth, thick, relatively randomly oriented, marginal ultimate venation looped; areoles well developed, random, polygonal, medium, veinlets lacking.

Discussion: the smallness of the leaf and its asymmetry suggest it could represent the leaflet of a compound (rosid?) leaf, but no evidence has so far been found to support this hypothesis. The base has a characteristic "notch" in one margin.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. The closest is *Quercus pachyphylla* Ett., from Grey River (c48.69), a small obovate-elliptic leaf with rounded apex and entire margin, but it has brochidodromous venation, a normal base and orthogonal reticulate tertiaries. There is some similarity to *Cassia pseudophaseolites* Ett., from Shag Point (zp93,94) and Cave Stream (zp21), with similar asymmetrical, microphyllous leaf form and pinnate secondaries. One of the leaves on zp93 (illustrated by Ettingshausen (1887) as Pl.6, Fig. 6a) has one secondary with equal branching. However, the leaves which are complete have acute apices and symmetrical obtuse normal bases. Furthermore, because of poor preservation, insufficient detail of fine venation is visible to allow direct comparison. *Santalum subacheronticum* Ett., from Shag Point (zp85), is a small elliptic leaf with truncate apex and normal base but no secondaries are visible. *Apocynophyllum affine* Ett., from Landslip Hill (c48.69), has too numerous secondaries and intersecondaries, and a normal base. (It

should be noted, in passing, that this fossil appears to me to be no different from that on c48.58, also from Landslip Hill, named *Dryophyllum dubium* and illustrated by Ettingshausen (1887) as PL.4, Fig. 6. *Cupanites novae-zeelandiae* Ett. from Grey River (zp125-132) and Pakawau (syntype not found, see Gregg 1975), is an asymmetrical leaf but has an acute apex and normal base. *Dalbergiophyllum rivulare* Ett., from Grey River (zp134), *Palaeocassia phaseolitoides* Ett., also from Grey River (zp133), and *Phyllites karamu* Hect n.n. (1886, Fig. 24A.2) have acute apices and normal bases.

The only foliar physiognomic type of Upchurch and Wolfe (1987) in which *P. asymmetricum* could be placed is Fig. 4.1a "microphyllous, not elongate (*Celastrophyllum obovatum*)". Hickey and Doyle (1977) describe *C. obovatum* Fontaine (within the *C. latifolium* Fontaine complex) as being "entire margined leaves with highly irregular brochidodromous venation and poor separation of the blade from the petiole ... and broadly obovate." However, *P. asymmetricum* is elliptic and has reasonably well-organised venation which is cladodromous. Among the morphotypes of Hickey (1984) and Crabtree (1987), *P. asymmetricum* has no counterparts.

Parvifolium crenatum sp. nov.

Holotype: CU 100.16#3 Cl.

Collection: Horse Flat, J.D. Lovis et al., April. 1979.

Diagnosis: leaf elliptic, apex obtuse, base slightly asymmetrical, decurrent, acute, secondaries very obvious, curvature uniform, increasing upward, ending in obtuse teeth in compound series, margin often apparently crenate, lamina very membranous.

Other material included: Horse Flat 100.08#6, #8, #12, and fragment beside #1, 100.11, 100.14 (fragment beside *Cladophlebis*), 100.15#5, 100.17#18 (fragment), 120.02 (on b only), 123.15; Ptilophyllum Ridge 522.76.

Number of specimens included: 12.

Plate 33B&C.

Derivation: from *crenatus* - Latin, meaning scalloped, referring to the margin.

Description: leaf simple, symmetrical, elliptic, microphyll, 4.0 (-6.5+) cm. long, 2.3 (-4.0+) cm. wide, L/W approximately 1.6, L/BTOW not observable; apex obtuse (95^0); base slightly asymmetrical, decurrent, acute 87^0 ; margin serrate, teeth rounded, apical and basal sides convex (A1 of Hickey, 1973) often apparently crenate, sinus angular to rounded, spacing irregular, series compound, on complete margin, teeth usually with hydathodes; lamina very membranous; petiole unknown.

Primary vein weak, straight, often grooved. Secondaries pinnate, simple craspedodromous, irregularly spaced but distance between decreasing upward, maximum on one side 9, mostly alternate, angle of departure moderate acute (45^0 -) 66^0 , upper and lower secondaries more obtuse than medial secondaries, very thick, some medial secondaries with branching lower, course sinuous, curvature uniform, increasing upward, parallel, intersecondaries lacking. Tertiaries angle of origin acute, random to orthogonal reticulate; highest order of venation observed third; areoles not observed.

Discussion: this form species is easily distinguished from all others described from the Clarence flora by its irregularly serrate margin with rounded teeth, and its strong, curved secondaries.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. It is somewhat similar to *Myrica proxima* Ett. from Malvern Hills, described by Ettingshausen from a single specimen (Ett.1887, PL.3, Fig.14; 1891, p.263) as "*marginē denticulatis; nervatione camptodroma*", but the fossil cannot be found for direct comparison (Gregg, 1975). It is also somewhat similar to *Alnus novae-zeelandiae* Ett., from Shag Point (zp61-63, c48.34) and Redcliffe Gully (syntype not found, Gregg 1975), but they have percurrent tertiaries and indistinct, small teeth. Other Ettingshausen species with which *P. crenatum* has some features in common are *Celastrophyllum australe*, *Daphnophyllum australe*, *Elaeodendron rigidum*, *Knightiophyllum primevum*, *Quercus nelsonica* and *Ulmophylon latifolium*.

The only foliar physiognomic type of Upchurch and Wolfe (1987) in which *P.crenatum* could be placed is Fig.4.1a, "microphyllous, not elongate (*Celastrophyllum obovatum*)", but *C.obovatum* has brochidodromous venation and poor separation of the blade from the petiole (see above under *P.asymmetricum*).

Hickey and Doyle (1977, p.25) report marginal teeth in two Potomac Group I species, *Protaephyllum dentatum* Fontaine and *Quercophyllum tenuinerve* Fontaine. "These teeth are irregularly spaced and doubly convex in shape (A1 of Hickey, 1973) and have a large glandular area near the apex". The former species is actinodromous, the latter obovate with weak, much branched secondaries. The only Zone II leaves with serrate margins are the actinodromous, ovate-cordate, lobate "*Populus*" *potomacensis* and unnamed simple, pinnately veined leaves (see Doyle and Hickey, 1976).

Crabtree (1987) has toothed-margined leaves in his Platanophyll (serrate), Protophyll (dentate), Sapindophyll (apparently cuconoid), Trochodendrophyll (crenate A1 chloranthoid), Menispermaphyll (lobate forms occasionally with teeth then craspedodromous, teeth modified chloranthoid type), Rhamnophyll (crenate-dentate, semicraspedodromous to teeth - acrodromous) and Dryophyll (serrate - palmately compound) morphotypes.

Hickey (1977,p.120), while describing the new fossil species *Betula hesterna* from the Early Tertiary of western North Dakota, states "families with members having simple craspedodromous venation are few in number. The elliptic to ovate shape, double serration of the margin and craspedodromous venation ... are characteristic of the Betulaceae. Within that family *Ostryopsis*, *carpinus*, *ostrea* [sic] and *Corylus* have cordate bases, and the lowest pair of secondaries set at a wider angle of divergence than those above. *Alnus* is characterized by an apically decreasing secondary interval, small marginal teeth, a lack of upturned marginal secondary veins and a larger number of secondaries than the fossil form. Many species of *Betula* show serrate, somewhat irregular marginal sculpturing; cuneate bases; and the same number and arrangement of secondary veins as that of the fossil". *B.hesterna* has (loc.cit.) "secondaries in 10 pairs; angle of divergence 45^0 to 70^0 , average 50^0 , stout, following a straight course to the margin where they are slightly upturned before entering the teeth, occasionally branched; teeth from 4 to 6 per middle secondary vein". Although Hickey refers to "10 pairs" of secondaries, only the lower veins are opposite, the degree of alternation increasing upward (see Hickey 1977, Pl.15, Fig.11, Pl.16, Figs.1,2).

Parvifolium crenatum, while conforming to the Betulaceae familial characteristics, displays a mixture of the characters used to separate the extant genera and cannot be satisfactorily compared with any of them. The secondary venation closely approximates that of *Chaetoptelea microphylla* (Newb.) Hickey (1977, p.122) from western North Dakota except in being alternate and less branched but the leaf

form, teeth and tertiaries are quite different. It has not been possible to discern the relationship of tertiaries to sinus in the Clarence specimens collected to date, preventing effective comparison with *Ulmus* or *Planera* though they appear to be closer to the latter.

Of other species with toothed margins described by Hickey (1977) from western North Dakota *Cercidiphyllum genatrix* (Newb.) Hickey is actinodromous, *Lamenonia borealis* Hickey has D-4 teeth, *Protophyllum serotum* Hickey is ovate, peltate, rounded or lobate with dentate teeth, *Stillingia casca* Hickey is ovate-lanceolate with eucamptodromous secondaries, *Meliosma longifolium* has dentate C-3 teeth, "*Amelopsis*" *acerifolia* (Newb.) Brown is palmately lobed with actinodromous secondary venation, *Temstroemites aureavallis* Hickey is ovate-lanceolate to narrow ovate with apex and base both acuminate and venation eucamptodromous, "*Viburnum antiquum* (Newb.) Hollick, and "*V*" *cupanioides* (Newb.) Brown have lower secondaries with three or more outer branches, *Dicotylophyllum anomalum* (Ward) Hickey has moderately close-set B-4 and C-4 teeth and brochidodromous venation, *D.hamameloides* Hickey has a dentate margin and semicraspedodromous secondary venation, *D.hebronensis* Hickey has a dentate margin and brochidodromous secondary venation, *D.mercerensis* Hickey has perfect acrodromous venation, while *Trochodendroides serrulata* (Ward) Wolfe is elliptic-oblate with perfect acrodromous venation.

Bell (1956, p.133) ascribed a fossil from the Blairmore Group of western Canada to *Celastrophyllum acutidens* Fontaine, remarking that it is "elliptical, petiolate, ... apex bluntly acute to right angled; margins more or less regularly crenodentate" but with "base cuneate on petiole" and "secondaries ... obscure distally but seemingly camptodromous." Insufficient detail is available to allow assignment of these Clarence fossils to this species.

Parvifolium emarginatum sp.nov.

Holotype: CU 100.12#1 Cl.

Collection: Horse Flat, J.D.Lovis et al., April, 1979.

Diagnosis: leaf wide elliptic, apex emarginate, base asymmetrical, decurrent, obtuse, secondaries eucamptodromous, margin entire, lamina chartaceous.

Other material included: Horse Flat 100.25#2.

Number of specimens included: 2.

Plate 33D.

Derivation: from *emarginatus* - Latin, meaning emarginate, referring to the apex shape.

Description: leaf simple, petiolate, asymmetrical, wide elliptic, microphyll, 6.0 cm. long, 3.4 (-4.0) cm. wide, L/W 1.7, L/BTOW 1.7; apex emarginate 320^0 ; base asymmetrical, decurrent, obtuse 142^0 (-165^0); margin entire, one side concave, hydathodes lacking; lamina chartaceous; petiole to 0.5 cm. long, 0.1 cm. wide.

Primary vein moderate, curved. Secondaries pinnate, eucamptodromous, angle of departure uniform, moderate acute (47^0 -) 52^0 , moderately thick, branching lower, course sinuous, curvature uniform, parallel, occasionally looping to join superadjacent secondaries at right angles, enclosed by tertiary loops, intersecondaries composite. Tertiaries angle of origin right angle, random reticulate; highest order of venation observed third; areoles well developed, random, irregular, large, veinlets lacking.

Discussion: the holotype is complete except for the base of the apical sinus. The condition of the primary vein termination therefore cannot be discerned. The other specimen consists of the proximal half of the leaf only. This species is somewhat similar to *Liriophyllites parvisinus* sp.nov., but differs in leaf form and symmetry, basal shape and symmetry, the lack of hydathodes, in chartaceous texture, the thickness, course and branching pattern of the secondaries, and in the lack of obvious forking of the midrib at the base of the sinus. If further specimens establish that the midrib does fork, this species may be relocated in *Liriophyllites*.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. *Dalbergia australis* Ettingshausen (1887, PL.5, Fig.5), described from a single specimen from Shag Point which has not been found (Gregg 1975), has an asymmetrical oblong form with apparently eucamptodromous secondaries and an emarginate apex of the *Liriodendropsis* shape (c.f. Hickey, 1984

leaf architectural group 20, Upchurch and Wolfe 1987, Fig. 4.1.p). *Daphnophyllum australe* Ettingshausen (1887, PL.4, Fig. 10), described from a single specimen from Shag Point which has not been found (Gregg 1975), is an obovate leaf with eucamptodromous secondaries. Ettingshausen (1891, p. 275), commenting on *D. australe*, states "the petiole appears to be joined to the lamina somewhat obliquely".

Loranthophyllum griselinia Unger (1864, PL.3, Fig. 13), which is very similar to *D. australe*, and *Phyllites quercoides* Unger (1864, PL.4, Fig. 11) are also obovate leaves with eucamptodromous secondaries. The first-mentioned Unger fossil clearly had an asymmetrical base. The second-mentioned Unger illustration is of a fossil lacking a base. However, neither of these Unger fossils can be found so direct comparison cannot be made.

Parvifolium membranaceum sp. nov.

Holotype: CU 100.01#2 Cl.

Collection: Horse Flat, J.D. Lovis et al., April, 1979.

Diagnosis: leaf narrow ovate, apex acute, base asymmetrical, decurrent, obtuse, margin irregularly crenate or wavy, lamina very membranous.

Other material included: Horse Flat 100.01#3, 100.05#4, 100.08#3#4, 100.10#4, 100.12#2, 100.17#11, 123.02(2)?; Alexander McKay Terrace 212.04?, 212.08?; East Quail Flat 330.40.

Number of specimens included: 9 plus 3 uncertain.

Plate 33E.

Derivation: from *membranaceus* - Latin, meaning membranous, referring to lamina texture.

Description: leaf simple, petiolate, symmetrical or asymmetrical, narrow ovate, microphyll, (4.5-) 5.8 (-8.0+) cm. long, (1.9-) 2.2 (-3.0) cm. wide, L/W (2.2-) 2.6, L/BTOW (2.3-) 2.6; apex acute 47^0 ; base asymmetrical, decurrent, obtuse 103^0 (-135^0); margin entire, irregularly crenate or wavy, occasional hydathodes; lamina very membranous; petiole to 1 cm long, $\frac{0.4}{\mu}$ cm wide.

Primary vein stout, slightly sinuous. Secondaries pinnate, cladodromous or semicraspedodromous, angle of departure uniform, moderate acute 59^0 , fine, branching lower from half way across lamina to near margin, course straight, curvature straight to uniform, parallel, occasional intersecondaries simple. Tertiaries angle of origin right angle, orthogonal reticulate; highest order of venation observed third, marginal ultimate venation incomplete; areoles well developed, random, polygonal, large, veinlets lacking.

Discussion: this form species is distinguished from others in the form genus by its narrow ovate form, acute apex, secondaries with a straight course, occasional simple intersecondaries and orthogonal reticulate tertiaries.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand suggests it is similar to *Ulmophylon planeraefolium* Ett. from Pakawau (zp149,151). However, ^{in *U. planeraefolium*} the tertiary veins have angles of origin which are acute exmedially and obtuse admedially, and are percurrent, sinuous, approximately at right angles to the midrib, and predominantly opposite. Also, the secondaries are unbranched thus preventing assignment of the Clarence fossils to that taxon. Other Ettingshausen species with which it has some characters in common are *Cassia pseudophaseolites*, *Cupanites novae-zeelandiae* and *Dalbergiophyllum nelsonicum*.

The only leaf architectural group of Hickey (1984) in which *P. membranaceum* could be placed is Group 8, "simple pinnately veined leaves with toothed margins and craspedodromous secondary veins" but the Clarence fossils lack distinct teeth and are only semicraspedodromous. The only foliar physiognomic type of Upchurch and Wolfe (1987) in which these Clarence leaves could be placed is Fig.4.1d "stenophyllous, serrate" but the same objections as those indicated with respect to Hickey's Type 8 apply here also.

Parvifolium obovatum sp.nov.

Holotype: CU 522.72#2 Cl.

Collection: Ptilophyllum Ridge, I.L.Daniel and J.D.Lovis, Feb. 1987.

Diagnosis: leaf narrow obovate, apex wide acute, base symmetrical, cuneate, acute, margin entire with occasional teeth, secondaries straight occasionally ending in teeth, lamina chartaceous.

Other material included: Horse Flat 120.05?; East Quail Flat 310.26; West Quail Flat 412.34; Ptilophyllum Ridge 522.56, 522.61#8, 522.72#1, 522.73#2, 522.76a#1.

Number of specimens included: 7 plus 1 uncertain.

Plate 33F.

Derivation: from *obovatus* - Latin, meaning obovate, referring to the leaf form.

Description: leaf simple, petiolate, asymmetrical, narrow obovate, microphyll, 6.0 (-6.5) cm. long, (2.0-) 2.7 (-4.0) cm. wide, L/W 2.2, L/BTOW 1.7; apex acute 78^0 ; base symmetrical, cuneate, acute (58^0 -) 61^0 (-78^0); margin entire with occasional teeth in distal part, occasional hydathodes in proximal part; teeth serrate acute, apical side concave, basal side straight (C-2 of Hickey, 1973), sinus acute, ending in a hydathode; lamina chartaceous; petiole 1 cm. long, 0.1 cm. wide .

Primary vein moderate, straight. Secondaries pinnate simple craspedodromous, angle of departure uniform to irregular, occasionally different ^{on either side of the midrib,}, moderate acute (34^0 -) $40/65^0$ (-68^0), moderately thick, occasionally branching lower, course straight, curvature straight, parallel, intersecondaries lacking. Tertiaries angle of origin acute or right angle exmedially, acute admedially, random reticulate; highest order of venation observed fourth; areoles well developed, random, irregular, medium, veinlets lacking.

Discussion: the leaves were apparently in a delicate state when deposited. The holotype has a wedge shaped medial portion and the base displaced, and the apical third folded at right angles to the rest of the leaf. All other specimens lack an apex. Specimen 522.76#1 is folded at right angles longitudinally. Basal

fragments were initially grouped with *Ficoidophyllum recurvum* despite lacking weak basal secondaries and having often irregular angle of departure of secondaries, but when the apex of the holotype was excavated, it became apparent that this group of leaves has an obovate leaf form and therefore belongs in a separate leaf form (see Section 9.4.1.b(i), Cluster 3b).

Comparison with fossils with an obovate leaf described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. *Daphnophyllum australe* Ettingshausen (1887, PL.4, Fig.10), described from a single specimen from Weka Pass, has similar leaf form and base but the Ettingshausen fossil has not been found (Gregg, 1975) so direct comparison cannot be made. *Elaeodendron rigidum* Ett., from Landslip Hill (c48.61), has a narrow acute, cuneate base but has a minutely crenate margin (see also comments under *Proteaceophyllum oblongum*). *Celastrophyllum australe* Ett., from Grey River (zp132), has a serrulate margin and camptodromous venation. *Knightiophyllum primaevum* Ett., possibly from Grey river (c48.36), has a sharply dentate margin and camptodromous venation. *Loranthophyllum griselinia* Unger (1864, PL.3, Fig.13) has an entire margin and camptodromous venation. Two species with a leaf form which is not obovate are otherwise somewhat similar to *P.obovatum*. The first, *Myrica subintegrifolia* Ett. from Shag Point (zp59), is oblanceolate and has a mucronate apex, entire margin and hypodromous venation (i.e. the secondary veins are not visible; see also comments under *Proteaceophyllum oblongum*). *Quercus celastrifolia* Ett., also from Shag Point (zp66), has venation similar to *P.obovatum* but is an elliptic leaf with a serrate-dentate margin.

The only leaf architectural group of Hickey (1984) in which *P.obovatum* could be placed is Group 8, "simple pinnately veined leaves with toothed margins and craspedodromous secondary veins" but the Clarence fossils have only occasional teeth. The only foliar physiognomic type of Upchurch and Wolfe (1987) in which these leaves could be placed is Fig.4.1a "microphyllous, non-elongate (*Celastrophyllum obovatum*)" but this species has brochidodromous venation and poor separation of the blade from the petiole (see above under *P.asymmetricum*). The only obovate, simple craspedodromous species described by Hickey (1977) from western North Dakota is *Carya antiquorum* Newberry, which has a closely serrate (C-4) margin and acuminate apex.

9.5.6.

Proteaceophyllum gen.nov.

Type: *Proteaceophyllum irregulare*.

Diagnosis: Leaf simple, petiolate, symmetrical, narrow elliptic to narrow oblong, microphyll to notophyll; base symmetrical, acute; margin entire or slightly crenate; secondaries semicraspedodromous or brochidodromous, departing at a moderate acute to right angle, weak compared to primary, zigzag or sinuous.

Derivation: from Proteaceae, the family, and *phyllum* - Greek, meaning leaf.

Discussion: Ettingshausen (1887,1891) assigned three species to the Proteaceae, viz. *Knightiophyllum primaevum*, *Dryandroides pakawauica* and *Dryandra comptoniaefolia*. The first (c48.36) is incomplete, lacking the apex and one margin. The other two are narrow elliptic. All have a stout midrib, weak camptodromous secondaries departing at a wide angle, and coarsely serrate or lobed margin. Holden (1982,p.88) remarks "Of these, *Knightiophyllum primaevum* resembles neither *Knightia* nor any of its close relatives, and the affinities of *Dryandroides pakawauica* are unclear". McQueen (1956,p.677), in discussing *Aspidium cretaceo-zeelandicum* Ett., remarks "Examination of the syntype at Canterbury Museum [zp137, see Gregg 1975,p.263] has shown that its classification as a fern is doubtful. - - - It may belong to the Proteaceous genus *Dryandra*, known from the Paparoa Coal Measures, from the upper Senonian of Pakawau (as *Dryandroides*, Ettingshausen,1887:68) and from possibly upper Senonian coal measures from Trellissick Basin."

Holden (1982) discussed the constituents of the Family Proteaceae presently found in New Zealand, and fossils previously ascribed to that family. She described three species from the Mid - Upper Miocene Longford Formation, *Knightia oblonga* Oliver, ?*Kermadecia merytifolia* Holden and *Longfordia banksiaefolia* Holden. The latter is a new genus and species established from a single fragmentary specimen. All three leaves are linear to oblong with moderate to stout midrib, weak

semicraspedodromous or brochidodromous secondaries departing at a wide angle, and an entire or coarsely serrate margin.

Krassilov (1977,p.155), while discussing his morphotype *Proteophyll* which is "characterised by dichopodial division of the leaf segments", noted "The possibility of ancestral Proteaceae in the Cretaceous cannot be ruled out". It should also be noted that pollen of proteaceous type has been reported in New Zealand rocks from the Late Cretaceous onwards (Couper,1960).

The Clarence fossils considered here are symmetrical, narrow elliptic to narrow oblong leaves, with semicraspedodromous to brochidodromous secondaries which are weak relative to the midrib and depart at a moderately acute to right angle. The margin may be entire or partly crenate. It is these characters which suggest proteaceous affinities, but while the gross venation pattern may suggest affiliation with genera ascribed to the Proteaceae, the absence of agreement of finer architectural features preclude attribution to any of the genera listed above. Therefore the form genus *Proteaceophyllum* is established to accommodate leaves exhibiting characters which suggest affinities with the proteaceous fossils previously described from New Zealand by Ettingshausen, Oliver and Holden, but which cannot be ascribed to any of the genera instituted by those authors.

Three species are recognised here from the Clarence flora. While *Proteaceophyllum lanceatum* and *P.oblongum* are each established from a single specimen, both are complete leaves with beautifully preserved venation the character states of which clearly separate them from all other leaf forms examined here (see Section 9.4). The three species may be distinguished by the following character combinations:

P.irregulare:

Narrow elliptic, apex acute, base cuneate or normal,
margin entire or with small crenations, secondaries
uniformly curved, semicraspedodromous, at an irregular
wide acute to right angle, with equal branching.

P.lanceatum:

Narrow elliptic, apex acute, base decurrent, margin
 crenate above entire below, secondaries abruptly
 curved, brochidodromous, at a moderate acute angle,
 with lower branching.

P.oblongum:

Narrow oblong, apex rounded obtuse, base decurrent,
 margin entire, secondaries recurved, brochidodromous,
 at a moderate acute angle, with equal branching.

Proteaceophyllum irregulare sp.nov.

Holotype: CU 522.09 Cl.

Collection: Ptilophyllum Ridge, I.L.Daniel and J.D.Lovis, Jan. 1986.

Diagnosis: leaf narrow elliptic; apex acute; base cuneate or normal; margin entire or with small
 crenations; secondaries uniformly curved, semicraspedodromous, angle of departure very irregular, wide
 acute to right angle, branching equal, parallel.

Other material included: Horse Flat 100.26#3, 100.08#1, 120.05; Alexander McKay Terrace 212.06,
 212.07, 212.08#8,#13, 212.10, 212.12, 212.13, 212.14, 212.15; East Quail Flat 310.23, 330.23, 330.40,
 330.41; Ptilophyllum Ridge 521.13, 522.18, 522.28, 522.30 (1 large specimen and 3 fragments), 522.31,
 522.48(3 fragments), 522.51, 522.52?, 522.61#2,#3,#5, 522.62#5, 522.77(2 specimens); Lower Seymour
 Stream 613.12?, 613.13, 613.20; Upper Seymour Stream 750.03?, 750.04, 750.05, 750.06?.

Number of specimens included: 39 plus 4 uncertain.

Plate 34A-C.

Derivation: from *irregularis* - Latin, meaning irregular, referring to the secondary vein angle of departure.

Description: leaf simple, petiolate, symmetrical, narrow elliptic, notophyll, (5.0-) 11.0 cm. long, (1.7-) 3.5 (-4.6) cm. wide, L/W (2.9-) 3.1, L/BTOW 1.8; apex acute 68^0 ; base symmetrical, cuneate or normal acute (45^0 -) 80^0 ; margin entire, occasionally with small crenations, occasionally some secondaries ending in a hydathode; lamina membranous; petiole to 1 cm. long, 0.1 cm. wide, base swollen.

Primary vein stout, straight. Secondaries pinnate, semicraspedodromous, branching at variable distance but usually halfway across lamina, upper branch generally joining with lower branch of superadjacent secondary, the vein from their union passing to margin and sometimes ending in hydathode, angle of departure irregular, wide acute to right angle, moderately thick, branching equal, course sinuous, curvature uniform, parallel, loops, if present, joining at right angle, enclosed by tertiary loops, intersecondaries composite. Tertiaries angle of origin acute exmedially, right angle admedially, random reticulate, highest order of venation observed third; areoles incompletely closed meshes, random, polygonal, large, veinlets lacking.

Discussion: the fossils included in this form species are a diverse set of leaves held together only by diagnostic characters which are variable. They may be able to be subdivided with further collecting and study.

Comparison with fossils with similar vein patterns described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. *Dryandroides pakawauica* Ett. from Pakawau (zp168) and *Myrica proxima* Ett. from Malvern Hills (syntype not found) have secondaries departing from the primary vein at close to a right angle. *M.proxima* also shows irregular secondaries sometimes looping to join the superadjacent secondary. However, both Ettingshausen species have finely serrate margins.

Phyllites novae-zelandiae Unger (1864,Pl.4, Fig.6, syntype not found) appears to be an oblong, entire-margined leaf with secondaries departing nearly at right angles but they are close, straight, unbranched, and appear to be camptodromous. *Phyllites brosimoides* Unger (1864,PL.4, Fig.12, syntype not found) appears to be an ovate leaf with simple craspedodromous secondaries departing at right angles but it has a finely crenate margin.

The leaf form and venation of *P.irregulare* superficially resemble those of *Knightia oblonga* Oliver, described by Holden (1982) from the Longford Formation (Mid -Upper Miocene), but the Clarence fossils lack a toothed margin. Furthermore, the base of *K.oblonga* from Kaikorai (Upper Miocene) is described by Oliver (1936,p.294) as being "widely diverging" which is distinctly different from the acute base of the present species. Some of the smaller leaves approach *Rogersia angustifolia* Fontaine but have higher ranked secondary venation.

Proteaceophyllum lanceatum sp.nov.

Holotype: CU 410.01(1) Cl.

Collection: West Quail Flat, I.L.Daniel and J.D.Lovis, Dec. 1984.

Diagnosis: leaf narrow elliptic; apex acute; base decurrent; margin crenate above, entire below; secondaries abruptly curved, brochidodromous, angle of departure more obtuse above, joining superadjacent secondaries at acute angle, branching lower, converging, enclosing tertiary loops lacking, areoles well developed.

Number of specimens included: 1.

Plate 34D.

Derivation: from *lanceatus* - Latin, meaning lanceolate, in the sense of A.P. de Candolle and Lindley, very narrowly elliptic (see Stearn, 1966, p.454).

Description: leaf simple, scarcely petiolate, symmetrical, narrow elliptic, microphyll, 7.5 cm. long, 1.6 cm. wide, L/W 4.7, L/BTOW 1.9; apex acute 31^0 ; base symmetrical, decurrent, acute 47^0 ; margin crenate above, entire below; lamina membranous.

Primary vein weak, straight. Secondaries pinnate brochidodromous, angle of departure moderate acute 57^0 , upper more obtuse, fine, branching lower, course sinuous, curvature abrupt, converging, joining superadjacent secondary at acute angle, not enclosed by tertiary loops,

intersecondaries composite. Tertiaries angle of origin right angle exmedially, acute admedially, orthogonal reticulate; areoles well developed, oriented, polygonal, large, veinlets lacking.

Discussion: the leaf form and secondary venation of *P.lanceatum* are similar to those of *Telopea speciosissima* R. Brown, *Myoporum laetum* Forst.f., and *Akania americana* Romero and Hickey, but it differs in other characters sufficiently to prevent it being assigned to any of them.

Comparison with fossils described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. There is some similarity to *Sapindus subfalcifolius* Ettingshausen (1887, PL.5, Fig.3, zp26; PL.6, Fig.2, not found), described from Upper Eocene/Lower Oligocene strata at Redcliffe Gully, particularly in the brochidodromous venation shown by the surviving fossil (zp26). However, the curvature of the leaf and lack of fine venation detail in *S.subfalciformis*, caused by poor preservation, preclude assignment of the Clarence fossil to that taxon.

Proteaceophyllum oblongum sp.nov.

Holotype: CU 411.41 Cl.

Collection: West Quail Flat, I.L.Daniel and J.D.Lovis, Dec. 1984.

Diagnosis: leaf narrow oblong; apex rounded obtuse; base decurrent; margin entire; secondaries recurved, brochidodromous, angle of departure uniformly moderate acute, joining superadjacent secondary at right angle, enclosed by tertiary loops, converging, branching equal, areoles imperfect.

Number of specimens included: 1.

Plate 34E.

Derivation: from *oblongus* - Latin, meaning oblong, referring to the leaf form.

Description: leaf simple, scarcely petiolate, symmetrical, narrow oblong, microphyll, 7.0 cm. long, 2.2 cm. wide, L/W 3.4, L/BTOW 2.3; apex rounded obtuse 96^0 ; base symmetrical, decurrent, acute 70^0 ; margin entire; lamina membranous.

Primary vein moderate, straight. Secondaries pinnate, brochidodromous, angle of departure uniform, moderate acute 50^0 , fine, branching equal, course zigzag, recurved, converging, joining superadjacent secondary at right angle, enclosed by tertiary loops, intersecondaries lacking. Tertiaries angle of origin obtuse exmedially, right angle admedially, orthogonal reticulate, highest order of venation observed third; areoles perfect, random, polygonal, large, veinlets lacking.

Discussion: it was thought at an early stage of the study that this leaf belonged in *P. lanceatum* but it consistently dissociated from it in computer studies. This is because they differ in their character states for the characters form, apex, margin and branching. The difference in apex and hence in leaf form may however be due merely to an abnormal state in *P. oblongum*.

Comparison with fossils described by Ettingshausen (1887, 1891) from Late Cretaceous and Early Tertiary sites in New Zealand fails to reveal any closely comparable species. *Elaeodendron rigidum* Ett. from Landslip Hill (c48.61) and *Myrica subintegrifolia* Ett. from Shag Point (zp59) have similar leaf form and basal shape. The coriaceous texture of both Ettingshausen fossils prevents detailed description of venation. Of *E. rigidum*, Ettingshausen (1891, p.281) writes "nothing is visible of the nervation except the strong straight primary nerve which is very pronounced nearly as far as the top of the leaf. From this primary nerve start at the middle distance of 1 cm. and at acute angles a few secondary nerves". Of *M. subintegrifolia* he writes (loc.cit.p.263) "From the rather strong primary nerve spring delicate secondary nerves, which run somewhat curved, and which have been preserved in few places". I have been unable to detect secondaries in either fossil. Furthermore, the former has a minutely crenate margin and the latter an acuminate apex, characters sufficiently distinctive to preclude assignment of the Clarence fossil to either taxon.

9.5.7. *Archaeopetala apiculata* sp.nov.

Holotype: CU 522.69 Cl.

Collection: Ptilophyllum Ridge, I.L.Daniel and J.D.Lovis, Jan. 1987.

Diagnosis: lamina obovate, length-to-width ratio approximately 1.5:1, apex apiculate (*obtusus cum acumine*), base contracting quickly to parallel sides, veins obscure.

Other material included: Ptilophyllum Ridge 522.37b (back of block).

Number of specimens included: 2.

Plate 35A-C.

Derivation: from *apiculata* - Latin, referring to the apex shape.

Description: lamina simple, obovate, length overall 6.0 cm., (base 1.0 cm., apex 0.5 cm.), width 3.5 cm., L/W 1.57; margin entire, contracting proximally quickly to parallel sides, rounded distally but ending in suddenly developed apex with rounded tip (*obtusus cum acumine*); lamina lacking prominent veins, obscure ridges radiating from base, outermost parallel to sides; texture smooth, perhaps fleshy.

Discussion: *Archaeopetala apiculata* is known from only one complete specimen. One other small fragment shows similar laminar characters. The complete specimen is appreciably smaller than *Archaeopetala obscura* Dilcher and Crane, has a very different apex and lacks the prominent veins of the Kansas species. In spite of these differences, the Clarence species may still be assigned to the genus *Archaeopetala* Dilcher and Crane (1984) since their diagnosis simply states (loc.cit.p.364) "Simple, laminar, entire-margined, isolated, fossil petal-like structures". Relationship to the plant *Archeanthus linnenbergeri* is implied but not stated, therefore the genus *Archaeopetala* is available for petal-like structures regardless of affinity. *The present fossils are here regarded as magnoliid.*

9.6. Discussion

The leaf fossils described above from the middle Clarence valley are all simple, broadly laminate leaves with reticulate venation and a well developed, narrow, terete petiole. All the leaves have secondary venation which is pinnate, some being craspedodromous, some with and some without teeth. Others have secondary venation which is camptodromous. In both groups some leaf forms have highly variable, poorly organised vein patterns which suggest primitiveness, while others have regular, well-organised patterns. All have third order veins, while some also have fourth order veins extending into well-organised areoles. Only four leaf forms have percurrent third order veins, the remainder having reticulate third order veins. None have characters typical of monocotyledonous leaves.

The leaf architecture generally corresponds in level of organisation to that of the Potomac Zone Iib (Middle - Upper Albian) leaves of Hickey and Doyle (1977), i.e. Rank 2 or 3 of Hickey (1971), except that none of the Clarence leaves are pinnately or palmately compound, and none have peltate, lobed or cordate bases. Of the 22 Clarence leaf form species, 15 are truly entire-margined, five have a lobed and/or crenate margin, and only two, *Latifolium serratum* and *Parvifolium crenatum*, have teeth.

Stratigraphic evidence suggests that at least some of the plants which bore these leaves were seasonally deciduous; beds containing large numbers of overlapping leaves are succeeded by beds barren of dicotyledonous leaves. For example, *Latifolium parvilobum* and *Ficoidophyllum oligodon* leaves occur in crevasse splays in large numbers suggesting a riparian plant showing seasonal deciduousness or perhaps suffering defoliation by wind storms. Ginkgoalean and bennettitalean leaves, generally accepted as being seasonally deciduous (Douglas 1969,p.157), show similar periodic deposition.

The Clarence dicotyledonous megaflora appears to have unique leaf forms present. None of the 22 Clarence leaf form species can be confidently correlated with any of the 38 Late Cretaceous and 19 Early Tertiary species described by Ettingshausen (1887,1891) from the more widely-known New Zealand megafloras, e.g. Shag Point, Pakawau, Grey River and Landslip Hill. The Ettingshausen species which are closest to Clarence species include *Alnus novae-zeelandiae*, *Cinnamomum intermedium*, *Daphnophyllum australe*, *Diospiros novae-zeelandiae*, *Dryophyllum nelsonicum*, *Myrica proxima* and *Ulmophylon latifolium*.

No coeval floras containing dicotyledonous leaves have so far been described from the Southern Hemisphere. A sequence of Australian deposits ranging from lower Neocomian to Albian in age appears, despite an earlier report to the contrary (Douglas, 1969), to be quite devoid of angiosperms. Cretaceous rocks are altogether poorly represented in southern Africa (Anderson and Anderson, 1985, p. 53). A deposit of Aptian age in Argentina (Romero and Archangelsky, 1986) has provided fossils so poorly preserved that description of only one dicotyledonous leaf form has been possible. It is quite unlike any of the Clarence leaves.

The Early Cretaceous dicotyledonous leaves described from the Northern Hemisphere appear to be quite different from the Clarence leaves. Only those species described from floras in western Canada (Bell, 1956), together with those from the Early Tertiary Golden Valley Formation of western North Dakota (Hickey, 1977), have, so far, been rigorously compared with the Clarence leaves. The species from these floras to which Clarence forms are closest include *Cinnamomoides ovalis*, *Corylus acutertaria*, *Magnolia magnifica*, *Persites angustus*, *Protophyllum semotum* and *Ternstroemites aureavallis*. However, none can be said to be closely comparable. This suggests that there were major differences between the Southern and Northern Hemisphere dicotyledonous leaf forms even at this early stage in dicotyledon evolution.

Furthermore, the floristic affinities of the Clarence leaves are obscure, although some may be interpreted as possibly belonging within a generalised family pattern. Thus, species here assigned to *Proteaceophyllum* and *Lauroidophyllum* have some characters typical of the Proteaceae and Lauraceae respectively. Furthermore, the species here assigned to *Latifolium* have a generalised "hamamelid" appearance (David Dilcher pers. comm., Nov. 1988). However, no unequivocal evidence is so far available which would allow any of the form species to be assigned to a particular modern family. Indeed, considering their age, being only some 20 million years after the earliest known dicots and 30 million years before the end of the Cretaceous Period, it would be most unwise to try so to categorise them (see also Section 1.6). Their taxonomically frustrating patterns of morphological variation, particularly numerous intermediates and overlapping generalised types, together with characters recurring in peculiar combinations, correspond well to Simpson's (1953, pp 228-229) description of a group undergoing active adaptive radiation.

CHAPTER 10. GENERAL DISCUSSION AND CONCLUSIONS

10.1. Introduction

Despite the fact that the taxonomic investigations detailed above elucidate only five of the eleven major plant groups present, a reasonably complete overview of the Clarence palaeomegaf flora has emerged. Indeed, the only major groups of leaves from the flora still to be studied are the ferns, podocarps and *Araucaria*. The remainder are of minor importance (Table 10.1). The actual number of taxa attributable to all of the unelucidated groups is presently unknown, but their lesser importance in the flora may be gauged from their limited occurrence (see Appendix 5). The study of fossil wood has not yet begun, apart from the sectioning of one petrified wood sample (see below). Palynological samples from some of the Clarence deposits have been investigated by J.I.Raine (see Reay 1980,p.68).

The flora is intriguing by virtue of its 1. apparently unique floristic composition and 2. luxuriant growth of a highly diverse suite of plants at very high latitudes. The first has important implications both for Cretaceous palaeobiogeography and for the evolution of the dicotyledons. With respect to the second, while it adds to the already considerable number of polar palaeofloras (see, for instance, Krassilov 1981, Douglas and Williams 1982, Jefferson 1983, Axelrod 1984, Wolfe and Upchurch 1987), more importantly it may yet prove to be the oldest high latitude flora containing angiosperms. As such, it may hold clues crucial to understanding vegetational changes which occur during periods of atmospheric and climatic changes that have become known as the "greenhouse state". It has become apparent (Fischer 1984) that the world climate was at the peak of just such a state during the Cretaceous Period.

10.2. Floristic composition

The Clarence palaeoflora consists of at least 60 taxa belonging to eleven major plant groups (Table 10.1, Column 1). Some of the taxa (see Sporne 1974,1975) represent archaic forms which were

initiated at least as early as the Carboniferous and either became extinct in the Cretaceous (Pteridospermales), or persisted to the present (Hepaticae, Pteropsida, Equisetales). Others, having their origins in the early Mesozoic, rapidly reached a peak of development in mid-Mesozoic times, and have since persisted as relicts (Cycadales and Ginkgoales) or, as in the case of the coniferous components (Araucariaceae and Podocarpaceae), have maintained an important presence in Southern Hemisphere forests till the present. Still others (Bennettitales and Pentoxylales) are restricted to the Mesozoic, and have been implicated in the origin(s) of the angiosperms (Crane 1985, Doyle and Donoghue 1986). Finally, the angiospermous component (here presumed to belong to the Magnoliidae) belongs within a plant group which ^{is generally regarded as having} made its initial appearance in the fossil record just some 20 million years prior to the deposition of the sediments of the middle Clarence valley, and which has, in the ensuing 100 million years, undergone very extensive evolution and radiation.

Hepatics (Plate 10A)

Two types of fossils from the middle Clarence valley may be referred to the Hepaticae. One is a thallose form, the other a leafy form but more detailed assessment has yet to be attempted.

Lycopods

A lycopod was reported (McQueen 1956) from the deposits but several recent collections of similar fossils suggest it may actually be a podocarp. Cuticular studies will serve to establish the true identity of this taxon.

Ephedraceae

A fossil here informally called a "linearphyll" closely resembles the Victorian fossil referred to *Isoetites?* sp. by Douglas (1973, PL.12, Figs.1,2). The specimen, GSV63921, and its counterpart, GSV63922, has since been deposited in the Museum of Victoria, Registered Number P167596, and has been reidentified as cf. *Ephedra* by A. Drinnan (M.Sc. thesis p.727, fig.5). The true identity of the Clarence taxon awaits further work.

Sphenopsids (Plate 10 E)

Isolated leaf sheaths and fluted stems found in small numbers at three sites in the Seymour Stream are undoubtedly *Equisetites* sp. Although limited in numbers, the occurrence of equisetaleans in the Cretaceous of New Zealand is of great interest. Previous records (Arber 1917, Retallack 1980) show their presence in New Zealand from at least the middle Triassic, but in spite of their ubiquity in time and space elsewhere in the world, they are entirely lacking from the Cenozoic of New Zealand (Raine and Pocknall 1983) and indeed from Australasia in recent times. The cause of their extinction in this region is unknown.

Ferns (Plate 10 B, C)

Of the ferns present, four species are referred to *Phyllopteroides* which belongs in the Osmundaceae (Cantrill and Webb 1987). A further six species of ferns have been tentatively identified, but further work will undoubtedly increase that number. However, their diversity is significantly lower than that of ferns in coeval floras (see Table 10.1). Furthermore, their frequency of occurrence, apart from the almost ubiquitous *Cladophlebis australis*, s.l. is limited (see Appendix 5).

Pteridosperms (Plate 10 F)

Although the fossils referred here to the form genus *Thinnfeldia* show some diversity of leaf form, they are believed to represent just one taxon. Fronds have been found which show variation of pinna shape along the rachis which includes most of the variation between various less complete fronds. The nearest form so far found in the literature is *Thinnfeldia* cf. *T. chunakalensis* Sah and Dev (as illustrated in Douglas 1969, p. 52). The Clarence fossil is probably a pteridosperm and most likely a corystosperm, which seem to have survived longer in the Australasian region than anywhere else (cf. Sporne 1974). It is relatively common at three of the Clarence locations.

Pentoxylaleans

One commonly found leaf form, *Taeniopteris stipulata*, is believed, despite the lack of confirmation by discovery of fructifications, to be pentoxylalean, a group formerly believed to be confined to the Jurassic (Sporne 1974) but now known also from the Early Cretaceous of Victoria

(Drinnan and Chambers 1985). If the present determination is correct, the New Zealand occurrences in the Clarence and at Pakawau (McQueen 1956) extend the range of the order to the mid and Late Cretaceous.

Bennettitales

The Bennettitales, a heterogeneous group with obscure origins in the Triassic, underwent rapid expansion in the Jurassic but were extinct in most parts of their former range by the mid-Cretaceous. In New Zealand, there was very low species diversity in this group in the Jurassic, just three species being recognised here (see Appendix 2). The present study indicates that the diversity had increased to at least eight species by the mid-Cretaceous, four of them in the *Pterophyllum* section of the order. Only one species can be referred to *Ptilophyllum*. Most have relatively *large* leaves, but occur in limited numbers.

Cycads

The Cycadales have obscure origins in the *Permian*, reached a peak of diversity and world-wide distribution in the *Mesozoic*, but after a decline across the Cretaceous-Tertiary boundary, are now restricted to Central America, southern Africa, eastern Asia and Australia. Two species are recognised in the Jurassic of New Zealand (Arber 1917). In the Clarence flora, their putative descendants, the simple leaved *Nilssonia elegans* and the pinnate-leaved *Nilssonia pseudocompta*, are of limited occurrence.

Ginkgoaleans

One ginkgoalean species, *Ginkgo cuneiformis*, is recognised in the Clarence flora where it forms a prominent element both in numbers of leaves and in their vertical and horizontal distribution. While ginkgoalean leaves and fruit have been reported from the Triassic of New Zealand (Retallack 1981) they are otherwise totally absent from known New Zealand Jurassic megaflores. Why this should be is unknown.

Conifers

The coniferous component of the flora is composed of several species of the Araucariaceae and Podocarpaceae. The former has its origins in the Triassic though the exact relationship within the family of ^{some} early forms from the Northern Hemisphere is unclear. The cuticular evidence here presented shows the presence of two species of *Agathis* which constitutes the earliest undoubted occurrence of that genus (cf. Stockey 1982). The other genus of the family, *Araucaria*, is represented by an as yet undetermined number of forms belonging to the sections *Columbea* (Plate 23C) and *Eutacta* (Plate 23D), the former now known only from South America and the latter from the south-west Pacific region. Several cone scales and seed scales (Plate 23F) have araucariacean affinities but have not yet been studied. Reay (1980,p.60) reported the presence of carbonised log and branch fragments and *in situ* stumps from the Warder Coal Measures at East Quail Flat. Changes in the river course have prevented inspection or collection of these. However a sample taken from the centre of a 0.5+ m. diameter ^{permineralised} log in the Willows Member at West Quail Flat has been sectioned (Plate 23E). The cell structure is typical of araucariacean wood and is very similar to that of *Araucarioxylon novae-zeelandii* described by Stopes (1914) from the Late Cretaceous at Haumuri Bluff. Other wood fossils collected are of twig or small branch dimensions and have not yet been studied.

All that can be said at the present time of the Clarence fossils referred to the Podocarpaceae (Plate 23A&B), a family with its origins perhaps as recent as the Jurassic, is that there may be as many as six species present, some of which show similarities of gross form to previously described fossil forms or to extant species. Their elucidation will be a major undertaking.

Angiosperms

Angiospermous leaves have been assigned to 22 new form species, all of which are considered to belong in the Magnoliidae. They occur in nearly all beds at all locations and constitute a major part of the flora, approximately equalling the gymnospermous component in both diversity and frequency. Only indirect indications of distinctive divisions above the generic level have been noted. Three species are referred to the form genus *Proteace ophyllum*, two to the form genus *Lauroidophyllum*, one to the form genus *Liriophyllites*, and resemblance to a "hamamelid" form is suggested for four others. The remainder

exhibit character combinations which have no obvious familial, or even ordinal, connotations. This appears to be a unique suite of dicotyledonous leaves.

Two tepal-like fossils are referred to *Archaeopetala apiculata* sp.nov., here considered to represent a magnoliid floral element.

Most of the deposits in the middle Clarence valley are stratigraphically below a series of basalt lavas, the bottom flow of which has been dated as 98 Ma. However one locality, West Quail Flat, lies stratigraphically above them. This deposit contains a suite of species somewhat depauperate compared with those below. Species only occurring here include the ferns *Phyllopteroides dentata*, *P.lanceolata* and *Taeniopteris arctica*, the bennettite *Otozamites* sp. and the dicotyledonous *Proteaceaophyllum lanceatum* and *P.oblongum*. Species occurring here as well as below the lavas include *Cladophlebis australis*, *Taeniopteris stipulata*, *Ginkgo cuneiformis*, *Agathis clarencianum* and the dicotyledonous *Ficoidophyllum recurvum*, *F.oligodon*, *Latifolium acutum*, *L.parvilobum* and *Parvifolium obovatum*, plus an undetermined but small number of species in *Araucaria* sect *Eutacta* and the Podocarpaceae. Most are relatively infrequent, only *L.acutum* and *L.parvilobum* occurring in significant numbers. Thus the flora appears to have undergone a significant reduction in species diversity during the volcanic episode.

Comparison of the composition of the Clarence flora with ^{Cretaceous} floras from other areas in New Zealand (Table 10.1, Column 2) is of only limited value since all of the latter are of Late Cretaceous (Coniacian - Maastrichtian) age. Furthermore, it has been shown in Chapter 9 that none of the Clarence dicotyledonous species can be referred to any previously described taxon. However, use of the census of known taxa collated (regardless of their legitimacy under the ICBN) by Raine and Pocknall (1983) allows rough evaluation of the possible changes occurring in the New Zealand palaeoflora during the Late Cretaceous. Raine and Pocknall (loc.cit.) did not subdivide the Cycadophyta/ Ginkgophyta. Nevertheless, it would appear that while the fern and non-coniferous gymnosperm components have remained relatively constant in numbers, their percentage contribution fell while that of the conifers and angiosperms, but especially the latter, increased dramatically. While the quadrupling of angiosperm species may in part be attributed to the tendency of earlier workers to oversplit taxa, it is still indicative of the rapid evolutionary radiation occurring during this time. Of significance in this respect is the

increasingly modern aspect of the dicotyledonous leaves in the Late Cretaceous which led to their being assigned (rightly or wrongly) by earlier workers to modern families and genera.

New Zealand was part of the southeastern seaboard of Gondwana until the Tasman Sea began to open approximately 80 million years ago. Thus, the extensive terrestrial sediments laid down in Victoria in the Early Cretaceous (Douglas 1969) were, at least in part, the hinterland of the "palaeo-Clarence" region. It could therefore be expected that there should be at least some congruence between the floras of the two regions. Indeed, this is the case. However, if congruence of species is expected, the differences due to coastal versus continental climates must not be overlooked. For instance, the lone species of *Ptilophyllum* in the Clarence flora had a relatively luxuriant leaf but, apart from one locality, is a minor element of the flora. In contrast, the 14 species from Victoria placed in *Ptilophyllum* by Douglas (1969,1982) were all of very small leaf size, and constitute a significant part of the flora. Furthermore, comparisons of the number of species in each plant group in the two regions must be done cautiously since the Clarence flora is from a geographically very restricted area and a geologically short time period. The Victorian flora is a compilation of a number of widespread localities ranging in age from Neocomian to Albian. Therefore, the percentage contribution of a particular plant group to a flora is of more significance in comparisons between these two floras than are species numbers.

The major differences between the Clarence and Victorian floras (Table 10.1, Columns 1 & 3) are the higher percentages of ferns and conifers and lower percentage of angiosperms in the latter. The overall difference between the two floras increases when it is realised that in the Victorian area *Equisetum*, pteridosperms and *Pentoxylon* had become extinct by the Albian (Douglas 1985). Furthermore, from Aptian to Albian times, there were significant alterations to the fern and lycopod constituents, the ginkgos declined markedly, and araucariaceans may have been largely replaced by podocarps (loc.cit.p.38). However if, as seems most probable, these changes in the Victorian flora are due to climatic changes, particularly increasing aridity, as is suggested by reduction in leaf size, then equally, the differences between the Clarence and Victorian flora are based on climatic differences. The major difference is, of course, the rich diversity and abundance of dicotyledons in the Albian in the Clarence area, and the paucity of angiosperms in the Victorian area even in the Upper Cretaceous Waarre Formation (Douglas 1969,p.285). While the situation in the Victorian area could be interpreted

as an expression of the difficulties experienced by early angiosperms in invading coniferous forests, this interpretation is rejected here in favour of environmental differences (see Section 10.3).

To establish the degree of similarity between the Clarence flora and those of the Northern Hemisphere, comparison is made with the floras described from western Canada by Bell (1956). They were chosen mainly because of contemporaneity, similarity of vegetational structure, and availability of literature. An equally interesting comparison would be with the Albian flora of eastern Russia, but the necessary literature has so far been unavailable.

By far the richest Cretaceous angiosperm megaflora known is that of the Dakota Group (Lesquereux 1892) which is virtually contemporaneous with the Clarence flora. The very large number of species described from the Dakota Group is certainly a grossly inflated figure, but serves to indicate the unique richness of this mid-Cretaceous flora. Revision of this flora is still in progress, and is not yet available, but David Dilcher, who is conducting this revision, has visited Christchurch and viewed the Clarence fossils. In his opinion there are no angiosperm species which are common to the two floras.

The comparison with palaeofloras from western Canada is made difficult by the fact that the numbers given in Table 10.1, Column 4 come from 17 formations ranging in age from Neocomian to Albian. Therefore comparison is best made using percentages. Inspection shows similarities of percentages (and often types) of cycadophytes and ginkgophytes, but again the major differences are in the percentages of ferns, conifers and angiosperms (in particular, dicotyledons). Again, as in comparison with Victorian floras, the first two are more abundant than in the Clarence flora, while the last is less abundant. However, the major difference becomes apparent when species are compared. The conifers of northern floras mostly belong to the Taxodiaceae, Cupressaceae or Cephalotaxaceae, while the angiosperms are magnolioid, salicoid, sapindoid or platanoid (Bell 1956; see also Hickey, 1982 and Chapter 9). Furthermore, *Pentoxylon* occurs only in the southern floras, while *Sagenopteris* (Caytoniales) occurs only in the northern flora. Thus it is apparent that, by the end of the Albian, or perhaps earlier, there had already been established differences in the Northern and Southern Hemisphere dicotyledonous floras which mirror those in the conifers (see also Section 10.3).

10.3. Environmental factors influencing growth at high latitudes

Since the first descriptions by Heer between 1868 and 1883 of numerous Tertiary fossil floras collected in Arctic regions, and his conclusion that they were typically of temperate form, writers have debated the problem of explaining the existence of forests and terrestrial large vertebrate faunas in polar palaeolatitudes. Axelrod (1984) pointed out that not only did Cretaceous - Paleogene floras grow within both Arctic and Antarctic Circles, but that today numerous species of trees and shrubs, both conifers and dicotyledons (though more of the latter), range as far north as 73° , i.e. well within the Arctic Circle.

Douglas and Williams (1982) introduced the southern polar forests to the debate and stated (loc.cit.p.171) "the existence of ... biotic communities through polar nights of about two to five months' duration is difficult to accept". Since plants did grow at polar palaeolatitudes, it is self-evident that conditions did not prevent them from doing so.

As indicated above, the fossil megaf flora of the middle Clarence valley contains leaf forms attributable to all the following plant groups: liverworts, ferns, equisetaleans, pteridosperms, cycads, bennettites, pentoxylaleans, ginkgoaleans, araucariaceans, podocarps and dicotyledons. The sediments in which they occur are fluviatile and lacustrine and were laid down in a coastal region of South Gondwana. The age of the deposits is late Albian/early Cenomanian. The palaeolatitude was high, being within the Antarctic Circle.

All of the plant forms except the dicotyledons had existed in the area since at least Jurassic times and while some may be considered relicts, many were undergoing evolutionary radiations. The combined polar wander path from palaeopole positions for various Antarctic, Australian and New Zealand rock units (Grindley et.al.,1981) passed across the eastern South Island of New Zealand during the Early Cretaceous, i.e. S.E.Gondwana had been slowly moving south since the Jurassic, subjecting the plants to increasingly more pronounced high-latitude conditions. Since this was accompanied by a gradual warming due to the changes of the Earth's climate towards the "greenhouse state" (see Fischer,1984, Fig.7.1), evolutionary adjustment to high latitudes should have been possible.

The genetic plasticity required to adjust to these changing conditions may be presumed to have varied between the plant types. Lack of sufficient plasticity could account for the decline (and eventual extinction) of, for example, the equisetaleans and pteridosperms. In contrast, the rapidly evolving

angiospermous plant form(s) could be expected easily to produce sufficient variation to exploit the high-latitude environment. Similarly, the *Pterophyllum* section of the Bennettitales appears to have been able to respond to the changing conditions with a radiation of species (see Chapter 6). To test this hypothesis, the "best response" of a plant to the physical conditions likely to be encountered must be assessed.

(see Section 1.5)

Palaeoclimatic evidence shows that the climate of polar regions in Cretaceous times was mild temperate and highly equable at least in coastal regions. Under these conditions two environmental factors impose adaptive pressure on plants living at high latitudes. Firstly, incident light was low for most of the growing season both in angle above the horizon and in intensity. It is proposed that this favoured development of leaves with a broad lamina with reticulate higher order veins and a petiole to achieve maximum effective light reception. Secondly, an extended annual dark season was accompanied by physiological drought conditions. It is proposed that this forced the plant, if perennial, to be either herbaceous with overwintering vegetative storage organs, or woody with seasonally deciduous foliage.

Incident Light

The initial requirement for achieving maximum light collection is to expand the leaf surface without increasing its bulk. This had been achieved earlier by *Glossopteris*, living at mid latitudes during the Permian, a period when the Earth's climate was ^{not} in the "greenhouse state". *Glossopteris* had an expanded lamina with only one order of anastomosing veins.

Creber and Chaloner (1984) decided that solar elevation and light intensity were not limiting factors in tree survival at high latitudes. Nevertheless, it is suggested here that the solar elevation in high latitudes being always below ca. 40° and at lower intensity than in temperate latitudes (June values being $24.4 \text{ MJm}^{-2}\text{day}^{-1}$ at 80°N compared with $31.5 \text{ MJm}^{-2}\text{day}^{-1}$ at 39°N , the former being enhanced by a longer day) will have great importance as an adaptive influence. Plant forms with more efficient light-collecting systems will be at an advantage. Creber and Chaloner considered a conical crown to be the most efficient (see below). However, leaf shape and attitude are probably more significant than plant habit. Thus, a broadly laminate leaf with a well-organised, ramifying complex of many orders of veins, allowing lateral extension of the lamina without loss of the close association of conducting and

supporting tissues with photosynthetic cells, will provide the most efficient leaf shape. Furthermore, a leaf with a petiole which allows adjustment of the lamina in attitude with respect to the stem and hence to direct incident light will be advantageous since a petiole "permits greater flexibility in the orientation of the broad lamina than does a broad leaf base, either for optimising exposure to light for photosynthesis or for reducing exposure to maintain heat balance and for reducing wind resistance" (Burger, 1981, p.193; see also Chapter 7).

The intensity of incident light at ground level will, of course, be dependent on plant habit insofar as it affects the vegetational stratification in a given area. Francis (1986,p.665) found that the Cretaceous forests of the Antarctic Peninsula (palaeolatitude 59° - 62° S) "were composed mainly of podocarp and araucariacean conifers. By the late Cretaceous, angiosperm trees were also present, particularly *Nothofagus*, forming the characteristic forest association of the southern hemisphere today". The only plant form for which evidence of the tree habit so far exists in the "palaeo-Clarence" area are the araucariaceans.

Creber and Chaloner (1984), having shown that the total annual solar input at high latitudes was adequate for tree growth, attempted to assess the crown shape best able to intercept incident light sufficiently well to achieve the estimated growth rate. They assumed (Creber and Chaloner, 1984,pp.431-433) that the Alexander Island (Antarctic Peninsula) trees described by Jefferson (1982) were conifers with conical crowns and formed a continuous canopy which virtually excluded light from the undergrowth. Similarly, Jefferson (1982,p.702) states "the low angle of incidence of the sun's rays would lead to extreme problems of shading in dense forests - - - . Ground-dwelling vegetation, of which there is considerable evidence, would also be shaded out by this tree cover". (This last sentence of Jefferson appears to be self-contradictory.)

In fact, most araucariaceans and many podocarps (and also the modern Southern Hemisphere genera of Cupressaceae such as *Libocedrus*) have tall, slender, cylindrical trunks with few branches generally confined to the upper portion and forming a spreading, diffuse crown. Indeed, araucariaceans and some podocarps exhibit cladoptosis (branch abscission). Furthermore, neither araucariaceans nor most podocarps commonly occur as continuous stands. Rather, they tend to occur in mixed forests (evidently with an understory of cycads, bennettites, pentoxylaleans etc., prior to the advent of

dicotyledonous ~~plants~~) forming an open canopy with emergent trees. Thus the amount of light reaching ground level is likely to have been greater than Creber and Chaloner and Jefferson have assumed.

Dark Season

Axelrod (1984,p.138) concluded that "polar regions were mild temperate and highly equable during the Cretaceous and Palaeogene. The problem of survival there is thus reduced to coping with the dark winter season". It is here suggested that two physiological processes must be considered in relation to the dark season, namely metabolism and transpiration. The amount of stored metabolites required to survive the dark season will be directly related to temperature, latitude and life history. Thus lower temperatures will decrease metabolic rate, higher latitudes will experience longer dark seasons, evergreens will require more metabolites than deciduous plants during the dark season, and perennials more than annuals. Since reduction of the amount of metabolites required to be stored during the growing season will be advantageous to plants, at higher latitudes deciduous perennials will have an advantage over evergreens, and annuals over perennials, provided, of course, that the growing season is long enough to enable completion of the life cycle.

The amount of transpiration occurring will also be directly related to temperature, latitude and life history, and under relatively mild temperate conditions will not be a problem. If, however, the substratum becomes frozen, as is possible under long dark seasons with clear skies, especially inland, the plant will be subjected to high water stress if aerial parts (especially leaves) are retained. This situation may be interpreted as physiological drought and will be equivalent to seasonal aridity. Thus xeric adaptations (e.g. thick cuticles, deciduous leaves, annual life history) will be advantageous. It is significant in this respect that various gymnospermous leaves found in Victorian Early Cretaceous deposits formed at similar palaeolatitudes to those in the Clarence area but in the continental interior, for example *Ptilophyllum* (see Section 10.2), have much smaller laminae, ^{more papillose stomatal apparatus} and thicker cuticles than comparable leaves from the Clarence deposits.

To survive the annual period of cooler, dark, and perhaps arid conditions, a plant with an expanded leaf form may adopt one of three basic strategies. It may be an annual, with survival from year to year being dependent solely on maturation and survival of the seed, an herbaceous perennial with overwintering vegetative storage organs, or a woody perennial with seasonally deciduous leaves.

For both perennial strategies, germination of seed and development of young plants must occur in one growing season, during which the young plants need to develop sufficiently to store enough metabolite to survive through the dark season. Since leaves are a major site of metabolism, their seasonal loss will reduce the metabolic rate of the plant as a whole and hence the amount of stored food required. Also, since they are the major site of water loss by transpiration, the absence of leaves during the dark season will obviate the necessity for foliar xeromorphic adaptations.

This suggests that annuals, herbs and deciduous woody plants will be better adapted to polar latitudes. Evergreen woody plants may be expected to be better adapted to temperate latitudes.

Since the time of Bailey and Sinnott (1916), and particularly through the work of Wolfe (1971,1978,1980,1987, and Wolfe and Upchurch 1987), a relationship between the state of the margins of leaves (particularly of dicotyledons) and climate has been recognised. It seems generally accepted that entire margins indicate a temperate climate while serrate margins indicate a cold climate. Furthermore, the former appears to be linked to evergreenness, while the latter is linked to deciduousness. Of the 22 dicotyledonous leaf form species described here from the Clarence flora, 15 are truly entire-margined, five have a lobed and/or crenate margin, and only two (*Latifolium serratum* and *Parvifolium crenatum*) have teeth. Several are believed, on stratigraphic grounds (see Chapter 9 and below), to be deciduous. Of the several non-dicotyledonous taxa believed to be deciduous, only *Pterophyllum rectipinnatum* could be considered to have a non-entire margin. Thus, there appears to be no correlation between deciduousness as indicated by leaf margin and deciduousness as indicated by stratigraphic evidence.

Conclusions

The Clarence flora contains a wide range of plant types the frequency of deposition and leaf form of which suggests they grew luxuriantly. In particular, the cycads, bennettites, *Thinnfeldia* and dicotyledonous elements of the flora have relatively large leaves compared with those of comparable species in Victorian Cretaceous sediments. Stratigraphic evidence suggests that *Taeniopteris stipulata*, *Agathis clarencianum*, *Ginkgo cuneiformis*, *Latifolium parvilobum*, *L.crenatum* and *Ficoidophyllum oligodon*, together with some of the other less numerous dicotyledons and at least some of the bennettites were deciduous. It would seem therefore that, apart from the coniferous elements (except for one *Agathis* species), the adaptive responses to the environmental factors influencing growth at high

latitudes proposed above have occurred in all the major plant groups in the Clarence flora. In particular, the dicotyledonous leaves are all simple, broadly laminate, pinnately reticulate-veined and have a terete petiole. No evidence has been found to suggest that any of the leaf forms were compound and none suggest an aquatic environment. Only two have well developed teeth, but several were probably deciduous.

It is suggested here that the presence in dicotyledons of intercalary meristem capable of producing a broadly laminate, petiolate leaf gave them an adaptive advantage which permitted their invasion of the high latitudes of South Gondwana as an integral part of the understory of an araucariacean/podocarp mixed forest. In contrast, the monocots of the Early Cretaceous were unable to cope with high latitudes and were therefore confined to the equatorial and low temperate latitudes of North Gondwana.

Under the influence of an extended dark season, some dicotyledons developed a woody, seasonally deciduous, perennial life history. This, together with the terete petiole, was a preadaptation which allowed the dicots to exploit not only high latitudes but also temperate and equatorial latitudes more effectively than all other plant groups.

APPENDIX 1

Notes on Palaeobotanical Drawings in New Zealand Literature (*See Addenda*)

In 1879, Hector(1878,p.536) presented a paper to the Wellington Philosophical Society which "gave a prodromus of a work on the fossil flora of New Zealand, containing descriptions and figures of about a hundred species." Earlier (Hector 1873,p.6) he had reported that "All the fossil plants found in New Zealand have been accurately drawn and printed by photolithography, fifty plates being now ready to illustrate a work on the fossil flora that is in progress." The "plates for the Memoir on the Flora were printed, but not issued" (Thompson 1913,p.12).

These "unpublished plates" are generally believed to have all been prepared by James Buchanan, but recent investigation of his life and works by Nancy Adams suggests otherwise. These investigations have brought to light original drawings by Buchanan of plant fossils from Mataura River prepared as Plate III for a work entitled "Geological Survey of Otago, Secondary Fossils, Plants" (Album 46, Otago Early Settlers Museum) but this work was apparently never published (N.Adams, pers.comm.)

Comparison of certain figures (Appendix Fig.1a-c) from this work with those in Hector's "unpublished plates"^(Appendix Fig. 1d-e) strongly suggests that only those figures depicting fossils on rock blocks are Buchanan originals.

Thus Figs.22,23 of Pl.VIII Hector are identical with Figs.7a,b of Pl.III Buchanan (*Sphenopteris*). Fig.7b of Pl.III Buchanan was reused in Hector's "Outline of New Zealand Geology" (1886b) as Fig.30A.9 (*Sphenopteris asplenoides*) but had been redrawn without rock and with some inaccuracies.^(Appendix Fig. 1g) Similarly the lower part of Fig.3 of Pl.III Buchanan^(Appendix Fig. 1c) has been redrawn without rock and with inaccuracies as Fig.24 of Pl.VIII Hector(*Appendix Fig. 1f*).

Fig.1 of Pl.III Buchanan (Appendix Fig.2b) depicts a block of rock bearing four pinnate fronds here interpreted as *Ptilophyllum acutifolium* (see Appendix 2.2). These fronds were poorly redrawn as five separate pieces as Fig.14 plus four unnumbered figures of Pl.VII Hector (regions I-V, Appendix Fig.2a). The source of the centre and upper right drawings is unknown. Note that region V of Hector's PL.VII is the counterpart of region V of Buchanan's PL.III. Close inspection of the lowest pinna to the right of the rachis of the right-hand frond (region III, Appendix Fig.2) of the two reproductions shows

careful detail of venation in Buchanan's Pl.III and simple shading in Hector's Pl.VII. Thus it seems evident that someone other than Buchanan copied unskilfully or traced the outlines of some Buchanan originals for use in Hector's "unpublished plates". The two styles are clearly illustrated in Pl.XXII Hector (Appendix Fig.1h) depicting dicotyledonous leaves from Shag Point, Buchanan being represented by excellent, detailed block drawings, the other by outline drawings of doubtful accuracy.

Similar line drawings are present in Ettingshausen's 1891 paper which was prepared in New Zealand after translation from the Austrian publication of 1887. The size of figures is reduced compared with the 1887 drawings, and the figures rearranged on the plates. Again the quality of the 1891 drawings is inferior to that of the 1887 drawings. Many discrepancies are apparent between the two works (see below), and between the 1891 drawings and the actual fossil (pers.obs.). The unreliability and lack of detail of many drawings in both Hector's "unpublished plates" and Ettingshausen's 1891 paper suggest their use for identifying fossils is strictly limited. Oliver (1950) used drawings from both of these sources often with varying size and no scale and revised names.

The practice of "picture matching", described by Dilcher (1974,p.13) as "unfortunate", has added to the confusion of the names and taxonomy of fossil plants in New Zealand literature. Three pinnate-veined leaves from Pakawau are illustrated in Figs.21-23 Pl.XXVI Hector (Appendix Fig.3a-c). They have a cuneate to rounded base and a regularly serrate margin bearing teeth with rounded apices. One of these, Fig.23, was redrawn for Hector 1886b as Fig.24A.1 (Appendix Fig.3d) where it was named *Patete scheffleri*. In this drawing the teeth are acute and the venation pattern has been altered by omitting some intersecondary veins. Oliver (1950,p.7, Pl.II, Fig.25) (Appendix Fig.3e) drew attention to this taxon, accepting the name from Hector 1886b but using Fig.21 of Pl.XXVI Hector which he attributed to "Buchanan (ined.)." (but see above). Oliver (loc.cit.) considers it "has no claim to be considered an araliad as both generic and specific names would seem to imply." He continues "More likely it belonged to the Tiliaceae. Ettingshausen's *Grewiopsis pakawauica* is apparently the same species." Ettingshausen's 1887 figure of *G.pakawauica* (Pl.IX, Fig.21) (Appendix Fig.3f) clearly shows a leaf with pinnate venation, a subcordate base and regular teeth with subrounded apices. The 1891 drawing of *G.pakawauica* (Pl.XXXII, Fig.21) (Appendix Fig.3g) has a margin with indeterminate teeth appearing to have acute apices. Although the apparent similarities of margin and of pinnate venation may have led Oliver to suggest *P.scheffleri* and *G.pakawauica* were the same species, their bases are very

different and the latter lacks an apex for comparison. On the basis of leaf shape, venation, base and margin *P.scheffleri* may equally well be said to be similar to *Fagus producta* (Ettingshausen 1887, Pl.IX, Fig.1) (Appendix Fig.3k).

McQueen (1951) apparently accepted Oliver's equivalence of *P.scheffleri* and *G.pakawauica*, and thus inclusion in the Tiliaceae, since he indicates the presence of this family in the Cretaceous of New Zealand. The only representative of this family in the modern N.Z. flora is *Enteleia arborescens* R.Br. which has actinodromous venation, a cordate base and a very different, irregularly crenate margin. It is interesting to note that Harland et.al.(1967) records the earliest Tiliaceae leaves as *Grewiopsis flabellata* (Lesq.) from the Cenomanian Dakota Formation. Muller (1981) records the earliest pollen of that family of *Brownlowia* type (*Discooidites borneensis*) from the lowest Eocene of N.W.Borneo, and of *Tilia* type (*Intratropipollenites pseudoinstructus*) from the Palaeocene of W.Europe and U.S.A.. The exact relationship of *Tiliaepollenites notabilis* from the Palaeocene of Queensland and New Zealand to the genus *Tilia* has yet to be established but is said to look tilioide (Muller 1981,p.45). Thus, the presence of Tiliaceae in the Cretaceous of New Zealand is in doubt.

Artocarpidium arberi Laurent was said to be similar to *F.producta* (but see comparison suggested above) by McQueen (1955) presumably because of their overall resemblance, but the margin of *A.arberi* is entire. *A.arberi* was described by Laurent (in Arber 1917,p.62,Pl.XIV) from two separate fragments (one apical, the other basal, see Appendix Figs.3h,i) occurring on a block from Pakawau (McQueen,1955). He referred it to the fossil genus *Artocarpidium* Unger to suggest affinity to *Artocarpus* (breadfruit), a genus in the Moraceae. Affinities are indicated by the camptodromous secondary venation and the polygonal network of tertiary veins. Oliver (1950,p.4,Pl.I, Fig.14) (Appendix Fig.3j) depicts a whole leaf of *A.arberi* but the source of his drawing is unknown. He describes it as having "the appearance of European beech leaves in which the marginal teeth are little developed. The straight parallel secondary nerves reaching the leaf margin [craspedodromous] especially recalls the beech family", a view apparently shared by McQueen (1955). As indicated above, *A.arberi* has an entire margin and camptodromous venation. Thus, the presence of *Fagaceae* in the Cretaceous of New Zealand based on Oliver's comparison is in doubt.

Appendix 2

Records and Revision of Selected Taxa

Several taxa which have been previously described from New Zealand Mesozoic localities are relevant to the taxonomy of leaves described in this thesis, but do not occur in the middle Clarence valley. They cannot, therefore, be included in the main body of the thesis. Their reporting and, where necessary, revision are given below.

2.1. Taeniopterid Taxa

Triassic Records

James Hector (1886a,p.31) lists fossils from Wairoa Gorge and Eighty-eight Valley, Nelson as *Taeniopteris* under the heading Otapiri Series which he placed in the Triassic (Rhaetic)(Hector 1886b,p.39), now included in the Otapirian local stage. No further details of the fossils are known. Ettingshausen (1887, 1891 and in Haast 1887) and Arber (1913b, 1917) also recorded various *Taeniopteris* species from the New Zealand Triassic, but their age determinations were the result of mixing of samples (see below under Jurassic Records).

The only authentic records of taeniopterids in the New Zealand Triassic are those of Retallack. From rocks of the Torlesse Supergroup, he (Retallack 1981,p.188, Fig.8) reported *Taeniopteris* sp.indet., a "Nilssonina-like" fragment from Long Gully, and (Retallack 1983,p.143, Fig.9C) *Taeniopteris* sp.indet., a fragment from near Benmore Dam which is "a little larger and more robust, and has less erect secondary venation". Later (Retallack, 1985), from rocks of the Murihiku Supergroup, he reported *Taeniopteris lenticuliformis* from Mataura Island and near Gore, *T.sp.cf.T.lenticuliformis* with secondary veins at 90° to the midrib from near Gore, *T.carruthersi* from Kaihiku Gorge, *T.sp.* with secondaries at 90° to a very thick midrib from Ben Callum, all from Southland, and *T.sp.* with very fine, close-set secondaries at 45° to the midrib from Wairoa Gorge, Nelson. They range in age from Smithian to Rhaetian (Malakovian to Otapirian local stages).

In view of the great differences between Triassic and later Mesozoic floras of Gondwana, these fossils are not considered in the revision of New Zealand taeniopterids presented below. Furthermore, the recent discovery at Potato Stream, Clent Hills of a Triassic flora containing a large number (presently in excess of 100 collection numbers) of taeniopterid leaves increases the complexity of the genus in the N.Z. Triassic beyond the scope of this review. These fossils are presently being studied by J.D.Lovis and E.A.Bond.

Jurassic Records

Beginning in 1870, Hector published lists of names of plant fossil species of Jurassic (his Mataura series, now within Temaikan local stage) age (Hector 1870, 1878, 1880, 1886a, 1886b). Included are eight species he ascribed to the genus *Taeniopteris*, (or *Oleandridum*), all but one of which are considered *nomina nuda* (Arber, 1913a, Mildenhall, 1970). The exception is *T.stipulata* Hector ex McQueen 1956 which is dealt with in Chapter 5.

In his "Outline of New Zealand Geology" Hector (1886b) published several sketches of indifferent quality of plant fossils. These are apparently inaccurate copies of drawings made by John Buchanan, prior to 1873 (Thomson 1913, p.11) or the plates prepared from these drawings but never published (see Appendix 1). Hector's sketches include "*Taeniopteris stipulata* (Pakawau)" (Hector 1886b, p.61, Fig.24A(3)) and "*Macrotaeniopteris lata* (Mataura Falls)" (op.cit.p.66, Fig.30A(4)). The latter was synonymised by Arber (1917, p.45) with *Taeniopteris crassinervis* (Feistmantel).

In 1884, fossil plant collections from Canterbury and Otago Museums were sent by Sir Julius von Haast and Professor T.J.Parker to Baron C. von Ettingshausen in Austria (Gregg, 1975). The collections were returned to New Zealand in 1886, and reported on by Haast (1887). Ettingshausen (1887b,p.367) listed seven plant macrofossil species from "Mt Potts" including "*Taeniopteris pseudo-vittata*, m", and ten species from "Clent Hills" including "*T.pseudo-vittata*" and "*T.pseudo-simplex*, m". Five species are common to both lists. Three, *Equisetum microdon*, *Taeniopteris pseudo-vittata* and *Palissya podocarpoides*, can confidently be synonymised with *Equisetites minutus* (Arber) Townrow, *Taeniopteris thomsoniana* Arber and *Mataia podocarpoides* (Ett) Townrow, all of which have been shown not to occur at Mt Potts (Retallack, 1980). *Baiera australis* n.n. Ettingshausen (synonym *Sphenobaiera robusta* (Arber) Florin^{side} Retallack, 1980) occurs only at Mt Potts. *Asplenium hochstetteri* Unger occurs

at Mt Potts as *Cladophlebis indica* (O. & M) Sahni & Rao (Retallack, 1980) and at Clent Hills as *Cladophlebis* spp. (Raine, 1982b). Thus it seems certain that, like Arber later, Ettingshausen had to deal with a set of specimens not reliably localised as originating from Mt Potts. Ettingshausen (loc.cit.) also records *T.lomariopsis* from Malvern Hills and *T.pseudo-simplex*, *T.lomariopsis* and *Macro-Taeniopteris affinis* from Mataura and Waikawa all dated by him as Triassic. All are *nomina nuda* (Arber, 1913a, Mildenhall, 1970) and all localities are Jurassic.

In the ensuing period of active geological exploration, various authors of geological reports referred fossils to the genus *Taeniopteris* but refrained from specific attribution. Hector however continued to use *Macrotaeniopteris lata* (sometimes as *Taeniopteris lata*) as a marker fossil for his Mataura Series (eg. Hector 1886b, p.65), and Park (1887, p.152,153) refers to its occurrence, together with *Taeniopteris stipulata* at Waikawa (see Thompson 1913, p.44,47,48 for a full list of specific references).

Críe (1888) referred fossils from Clent Hills, Wairoa Gorge and Mataura to *Macrotaeniopteris zeelandica* n.n.

In 1912, E.A.N.Arber of Cambridge received fossil material from the New Zealand Geological Survey collection and from the Canterbury Museum, all or some of which had already been seen by Ettingshausen. In addition Arber received material freshly collected by D.G.Lillie, Biologist on the "Terra Nova", the ship of Captain Scott's Second Antarctic Expedition. In November 1911, Lillie, in conjunction with R.Speight of Canterbury College, collected plant fossils which Arber presumed to have come only from Mt Potts (Arber, 1913b). It has been shown however (Blaschke and Grant-Mackie, 1976; Retallack, 1980; Raine, 1982a) that the collection was mixed, coming from both Tank Gully at Mt Potts and Haast Stream at Clent Hills.

In his major work "The Earlier Mesozoic Floras of New Zealand" Arber (1917) listed 9 species from Mt Potts and 8 species from Clent Hills. Five of these, *Phyllothea minuta* sp.nov., *Taeniopteris thomsoniana* sp.nov., *Elatocladus conferta* (O. & M)^{Arber}, *Dictyophyllum acutilobum* (Braun)^{Schenk} and *Cladophlebis australis* (Morr.)^{Halle} are common to both lists. Retallack (1980, p.31) stated that the first four species listed above "have never been found in collections from Tank Gully after Arber's record". Raine (1982a) having inspected all of Arber's material reached the same conclusion and stated (op.cit.p.2) that

"The rock matrix from both localities is very similar being a dark grey carbonaceous argillite, hence the probability of mixing of collections".

Arber (1917) recognised five species of *Taeniopteris* from various "Jurassic" deposits throughout New Zealand. Leaves which were "rather small, spatulate" with "apex broadly rounded" (op.cit.p.47) from Clent Hills he described as *T.thomsoniana* sp. nov. He synonymised *Macrotaeniopteris lata* Hector from Mataura Falls with *Taeniopteris crassinervis* (Feist). Leaves "broadly or narrowly linear" with "Lateral nerves fine, close" (op.cit.p.47) from Waikawa he placed in *T.vittata* Brong. Leaves which were "very long, linear, parallel sided ... edges straight" (op.cit.p.46) from various South Island Jurassic localities he placed in *T.daintreei* McCoy. Leaves which (op.cit.p.44) "in some respects very closely resembles *T.daintreei* McCoy in habit ... [but] ... differs, however, in the nervation, the nerves being conspicuous and comparatively distant" and which have distinctive U shaped forking of lateral nerves (pers.obs.) he placed in *T.arctica* Heer. Arber also quoted Heer's diagnosis for the fronds "from the Cretaceous of Greenland" which includes in part "soris rotundatis, biseriatis, nervo medio approximatis". It is thus clear that Arber believed that these New Zealand leaves belonged to a fern.

He gives the locality from which these fossils had been obtained as "Waikato Heads (Neocomian)" and states (loc.cit.) "Fragments of this frond also occur on the large specimen figured in Plate XIV, but are not seen in the photograph". This "large specimen" (B161/30) also bears dicotyledonous leaves and was shown by McQueen (1955) to have come from Cretaceous strata at Pakawau. Of the leaves illustrated by Arber as belonging to *T.arctica*, only that figured in Plate VI, Fig.1 remains in the New Zealand Geological Survey collection (B65.11).

The leaves included in Hector's unpublished plates as PL.XV, Fig.8 (B161.5), Fig.11 (B65/16); PL.XVIa, Fig.34 (B65.11 IVB), Fig.35 (B65.12), Fig.41 (B65.15) all show venation similar to that of Arber's *T.arctica*. All are labelled as being from "Waikato Heads" but all have the matrix characteristic of the Pakawau deposits. In addition nearly every block of N.Z.G.S. collection B74, localised as originating from Pakawau and having the same matrix bears *T.arctica* and *T.stipulata*. Leaves actually from Waikato Heads (eg. Hector unpublished plates PL.XV, Fig.1 (B77.5)) correspond well with *T.daintreei* of Arber from South Island localities.

W.N. Edwards (1934, p.97) transferred to *Taeniopteris spatulata* McClelland the species recorded by Arber as *T.daintreei* on the grounds of priority. He also placed there the "Waikato Heads"

material which Arber had placed in *T.arctica*. He also suggested (op.cit.p.98) that the "fronds with a fine close venation from Waikawa described by Arber as *T.vittata* may be only an extreme form of the same [*T.spatulata*] species".

Blaschke and Grant-Mackie (1976, p.939) used population studies based primarily on lamina width to distinguish two species of *Taeniopteris*. Leaves from Port Waikato were assigned to *T.daintreei* McCoy. Leaves from Clent Hills were assigned to *T.thomsoniana* which they maintain is the only species occurring there (but cf. Ettingshausen, 1887b; Arber, 1917).

It is reasonable that Blaschke and Grant-Mackie discount Arber's use of *T.arctica* Heer for their Port Waikato leaves on the grounds of structure, age and location but the "possible presence of sori" (op.cit.p.936) on *T.arctica* does not preclude its attribution to the form genus *Taeniopteris* (eg. see Edwards 1926, p.124).

Having correctly pointed out (loc.cit.) "that Arber's (1917) allocation of the Port Waikato population to *T.arctica* was based on a specimen subsequently found to have come from upper Cretaceous strata of Pakawau, Nelson" Blaschke and Grant-Mackie failed to recognise there are two taeniopterid taxa at Pakawau and incorrectly state that "The New Zealand hypotype of *T.arctica* (from the upper Cretaceous at Pakawau) also fits into the description of *T.daintreei* from Victoria, but population studies allow separate recognition of the Pakawau form as *T.stipulata* (McQueen 1956)." In spite of this statement they include "1917 *T.arctica* Heer: Arber" in their synonymy of *T.daintreei* McCoy.

Blaschke and Grant-Mackie (loc.cit.) incorrectly listed "1934 *T.spatulata* McClelland; Edwards ..." in their synonymy of *T.daintreei*. It would have better served the same purpose had they listed "1917 *T.daintreei* McCoy; Arber p.46 PL.VI, Fig.5" instead (see under W.N.Edwards above). They also incorrectly included "1850 *T.spatulata* McClelland" in their synonymy (cf. Douglas 1969, p.53; Drinnan and Chambers 1985, p.90).

Douglas (1969, p.57) maintained *T.daintreei* from Victoria, Australia as a separate taxon from *T.spatulata* s.str. (= *Nipaniophyllum raoi* Sahni for silicified Indian leaves) on cuticular differences. Drinnan and Chambers (1985, p.92) have shown the differences between *T.daintreei* and *T.spatulata* to be not as great as Douglas (1969) thought, but in view of the association of *T.daintreei* with fruiting structures (*Carnoconites cranwellii* Harris) different from those associated with *Nipaniophyllum raoi* Sahni (ex *T.spatulata* McClelland), they maintain *T.daintreei* McCoy as a distinct species. They retain it

in the genus *Taeniopteris* until organic connection is proved. The *T.daintreei* of Blaschke and Grant-Mackie (1976) is included in their synonymy.

Raine (1987) re-examined material from Manganui Valley Awakino District, North Island, first identified and listed by Ongley (in Henderson and Ongley, 1923) and thought at that time to be Triassic. The deposits are shown to be Jurassic and the macroflora to include *Taeniopteris daintreei* (Raine 1987, p.127, PL.1, Figs.2,3,4).

Raine (in Johnston, Raine and Watters, 1987) also described macrofossils from the Marybank Formation at Marybank, East Nelson. He referred leaves which were (loc.cit.p.241) "spathulate with short apical portion (obtusely rounded in the single apex seen) and long tapering basal part" to *T.thomsoniana*. Fragments with (loc.cit.) "a midrib 5-6 mm. wide, and lamina over 50 mm. from midrib to margin" and secondary venation "at right angles to the midrib, and seldom bifurcate" he compared (because of the incomplete nature of the leaves) with *T.crassinervis*.

Nilssonia elegans is the name given by Arber (1917) to taeniopterid-like leaves with lobed margins from Mataura Falls. Edwards (1934) records their presence at Waikato Heads.

Systematics

Class Cycadopsida

Order Pentoxylales

Taeniopteris A.Brongniart 1828 emend. Harris 1932

Taeniopteris daintreei F.McCoy 1874

Synonymy:

1873 unnamed: Hector "unpublished plates" PL.XII, Figs.10, 12; PL.XIII, Fig.17,18; PL.XIV, Figs.22,22a, (Waikawa). PL.XV, Fig.1 (Waikato Heads).

1887 *T.pseudo-simplex* Ettingshausen n.n.

1880 *T.stipulata* Hector n.n.

1887 *T.stipulata* Park n.n.

1917 *T.daintreei* McCoy: Arber p.46, PL.VI, Fig.5 (Many South Island localities including Clent Hills).

1917 *T.vittata* Brongniart: Arber p.47, PL.IV, Fig.4; PL.VI, Figs.2,3 (Waikawa).

1969 *T.daintreei* McCoy: Douglas p.53, PL.17, Figs.3,4;

PL.18, Fig.3; Figs.1,1; 1,51-55; 1,65 (Australian).

1976 *T.daintreei* McCoy: Blaschke & Grant-Mackie p.936,

Figs.2,3,4 (Port Waikato).

1985 *T.daintreei* McCoy: Drinnan & Chambers p.90, Figs.1-4

(has Australian synonymy prior to Douglas 1969).

1987 *T.daintreei* McCoy: Raine p.127, PL.1, Figs.2,3,4

(Manganui Valley).

Lectotype NMV P12270, Natl.Mus.Vict.

Diagnosis

As by Drinnan and Chambers 1985, p.90.

Discussion: the description of Drinnan and Chambers (1985) is accepted but certain details require comment. The leaf is linear/elliptic i.e. it has approximately parallel edges for a considerable part of the leaf, then gradually tapers to apex and base. The width is given as 1-3 cm which encompasses all described N.Z. taeniopterids except *T.crassinervis* (Feist) Arber and cannot be considered diagnostic. The apex is usually acute but occasionally may be acuminate or obtuse. The base is very acutely decurrent; in fact the acropetal increase in lamina width is so gradual, it is difficult to distinguish a point where it may be said that the "petiole" ceases and the midrib/lamina complex begins. The secondary vein angle (70^0 - 90^0) and density (15-30 per 1 cm. of lamina) encompasses all N.Z. taeniopterids except

for the vein density of some *T.thomsoniana*, most *T.stipulata* and *T.crassinervis*. The secondary veins usually fork once close to the midrib, occasionally a second time before meeting the margin. The midrib is prominent and, while it persists to the leaf apex, it narrows in the distal third of the leaf. The lamina is occasionally undulate.

Remarks

The taeniopterid leaves from Waikawa described by Arber (1917) as *T.vittata* and those illustrated from the same locality in Hector's "unpublished plates" are noticeably wider (mean lamina width of 13 figures = 1.5 cm., range 1-3.3 cm.) than those recorded by Blaschke & Grant-Mackie from Port Waikato as *T.daintreei* (mean 0.6 cm., range 0.3-2.5 cm.). It was initially thought they could be separated as a distinct species on width and secondary vein density. However the ranges of these characters as defined for *T.daintreei* by Drinnan & Chambers (1985) plus their linear/elliptic shape and acute apices (none shown by Arber but present in Hector's "unpublished plates") prevent such a separation.

Harris (1964 p.35, 1969 p.67) explained the confusion associated with *Nilssoniopteris vittata* (Bennettitales) and *Nilssonia tenuinervis* (Cycadales) and included Arber's leaves in the former. His diagrams however leave no doubt that on leaf form alone, these fossils should be placed in the latter. Since it is now apparent (see Chapter 5) that leaves with such an extended base are more likely to be pentoxylalean than bennettitalean, the inclusion of the Waikawa leaves in *T.daintreei* is of value.

Raine (in Johnston, Raine and Watters 1987, p.291 and Table 2) states that the Waikawa material separated by Arber as *T.vittata* contains specimens similar to the fossils from Marybank which he identified as *T.thomsoniana*. However, their leaf and apex shape, as noted above, prevents their reference to *T.thomsoniana*.

N.Z. Occurrence and Age

Waikato Heads (Port Waikato): Puaroran (uppermost Jurassic).

Clent Hills: Temaikan - Puaroran (mid-upper Jurassic)

Waikawa, Malvern Hills and other South Island localities: Teraikan (Middle Jurassic)

Manganui Valley (Awakino District): early-mid Jurassic.

Taeniopteris thomsoniana E.A.N. Arber 1917

Synonymy:

1873 unnamed: Hector "unpublished plates" PL.II, Figs.8,10, 13,14,16 (Clent Hills).

1887 *T.pseudovittata* Ettingshausen n.n.

1913 *T.daintreei* (McCoy): Arber p.346, PL.8, Fig.5 (figure, no description).

1917 *T.thomsoniana*: Arber p.47, PL.VI, Fig.4 (type) PL.VIII, Figs.4,7 (Clent Hills) (name, description and figures).

1976 *T.thomsoniana* Arber: Blaschke & Grant-Mackie p.938, Figs.5,6 (Clent Hills) (emended description).

1987 *T.thomsoniana* Arber: Raine in Johnston, Raine and Watters p.291, Figs.6D,7C (Marybank) (description and figures).

Holotype: V 15693, BM(NH) (Arber 1917 PL.VI, Fig.4).

Diagnosis:

As by Blaschke and Grant-Mackie 1976, p.938.

Discussion: the emended diagnosis of Blaschke & Grant-Mackie correctly gives the leaf shape as oblanceolate (cf. Arber 1917, p.47 "spathulate") which seems to distinguish *T.thomsoniana* from other taeniopterids (but cf. Drinnan and Chambers 1985, Fig.4). The lamina decreases in width towards the obtuse apex and towards the very acute decurrent base from the same point within the distal third of the leaf. Thus there is no significant portion of the leaf with parallel margins. Furthermore, taper to the apex is rapid.

The secondary veins arise at more than 80^0 to the midrib at a density within the range for *T.daintreei* except for a few specimens with greater density. Approximately 60% of secondary veins fork once near the midrib (more than in *T.daintreei*), some occasionally a second time near the margin. The midrib is usually less than 1/10 the width of the lamina ie. is less prominent than in *T.daintreei*. The lamina is usually rugose, with wrinkles parallel to the secondary veins and irregularly spaced along the leaf (pers. obs.). Large numbers of usually fragmented leaves occur together with other taxa, in vertically restricted but numerous horizons (pers.obs.).

Remarks: the characters most useful in separating *T.thomsoniana* from other taeniopterids in hand specimen is the oblanceolate shape, obviously obtuse apex and rugose lamina. Blaschke & Grant-Mackie emphasized overall size and in particular lamina width as separating *T.thomsoniana* of the Clent Hills from *T.daintreei* of Port Waikato. While their data support the hypothesis that there are different populations (t-test $p < 0.001$), a similar comparison of the lamina width of 35 individual leaves of *T.stipulata* from the Clarence valley with the Clent Hills population suggest they are from the same population (t-test $p \ 0.2 > x > 0.1$). One of the greatest difficulties in using lamina width is obtaining the "true" width of an incomplete leaf.

Occurrence and Age:

Marybank (Nelson): (late Jurassic-early Cretaceous).

Clent Hills: Temaikan-Puaroan (mid-upper Jurassic)

Order Bennettitales

Taeniopteris Nathorst 1909 (Diagnosis Harris 1969)

Taeniopteris crassinervis (Feistmantel) Arber.

Synonymy:

1873 unnamed: Hector "unpublished plates" PL.V, Figs.1-3, PL.VI, Fig.7 (Mataura Falls).

1886 *Macrotaeniopteris lata*: Hector p.66, Fig.30A(4) (name and inaccurate sketch) (Mataura Falls).

1887 *M.affinis*: Ettingshausen p.42 (no description or figure).

1888 *M.zeelandica*: Crie (no description or figure).

1917 *Taeniopteris crassinervis* (Feist): Arber p.45, PL.IX, Fig.4; PL.X, Figs.1-3,5 (diagnosis) (Mataura Falls).

1950 *T.crassinervis* (Feist): Oliver p.8, PL.I, Fig.7.

1987 *T.cf.T.crassinervis* (Feist): Raine in Johnston, Raine and Watters p.291, Figs.6G,H;7D,G (Marybank) (description and figures).

Holotype: B64.6, NZGS Coll., Arber 1917 PL.X, Fig.1.

(N.B. Hector 1873 PL.V, Fig.1 = Hector 1886 Fig.30A(4) = Arber 1917 PL.X, Fig.1 = Oliver 1950 PL.I, Fig.7).

Diagnosis:

as by Arber 1917, p.45.

Remarks: the coarseness of the secondary veins and the width of midrib of *T.crassinervis* are unique among New Zealand taeniopterids. Raine's reluctance (Johnston, Raine and Watters p.291) to identify the fragments from Marybank with *T.crassinervis* is here considered to be unnecessarily cautious.

It is here proposed that the generic attribution of *T.crassinervis* should be revised to *Nilssoniopteris* Nathorst (see Chapter 5). This proposal is based on its overall similarity to *Nilssoniopteris*

sp. described from the middle Clarence valley, which is established (admittedly shakily) as a bennettite on cuticular micromorphology. They differ only in leaf size, midrib and vein dimensions, and in age. It should be noted that leaf size is discounted by Arber (1917,p.45) as a useful distinction between *Taeniopteris* and *Macrotaeniopteris*. Furthermore, the diagnosis given by Arber differs from that for *Nilssoniopteris major* by Harris (1969, p.72) only in leaf dimensions and margin. The young leaf illustrated by Harris (1969, Fig.33A) bears a striking resemblance to that in Hector's unpublished plates PL.V, Fig.2.

Distribution and Age

Marybank, (Nelson): (late Jurassic-early Cretaceous).

Mataura Falls, Waikawa: (Middle Jurassic).

2.2. Pinnate Cycadophyte Taxa

Of the drawings of fossil leaves in the N.Z.G.S. collection prepared for Hector's "unpublished plates" (Thompson, 1913, p.11), only nine represent pinnate cycadophytes (see Appendix 1 for a detailed discussion of the history of the drawings). They all appear on Pl.VII (see Appendix Fig.2), are labelled as originating from Mataura Falls, and appear to represent two distinct taxa.

The upper seven drawings (Figs.14 and 15 plus 5 unnumbered) represent pinnate leaf segments with pinnae overlapping the one below or at least in contact with each other. Pinnae are opposite to subopposite to alternate, and have acute apices. Fig.14 (B73/19) plus 4 of the unnumbered drawings (regions I-V, Appendix Fig.2a) were copied from a drawing of a complete block bearing four fronds (Appendix Fig.2b) prepared by Buchanan for Plate III of "Geological Survey of Otago, Secondary Fossils, Plants" (see Appendix 1). These fronds were named "*Zamites Matauriana* Hector" in the legend to Buchanan's Pl.III. Three drawings are of apical segments with pinnae diminishing in size upwards. The other drawings are of medial segments, three of which show the rachis with borders, implying the pinnae are attached to the top (away from the observer) of the rachis. They are here interpreted as

Ptilophyllum acutifolium Morris ex Arber. Arber (1917,p.53, Pl.XI,Figs.1,2,5) also described and figured *Ptilophyllum acutifolium* Morris from Waikawa.

The lowest two drawings of Hector' "unpublished plates" Pl.VII, (regions Ai and Aii of Appendix Fig.2a (B73/30)), represent leaf segments with a clear gap between pinnae even when the lower basal angle of a pinna is slightly expanded (decurrent). Pinnae are opposite to alternate and appear to be attached to the sides of the rachis. They are here interpreted as *Pterophyllum matauriensis* Hector ex Arber.

One of the medial segments of the upper group, Fig.15 (region B, Appendix Fig.2a), was used as the basis for a sketch by Hector (1886b,p.66, Fig.30A(7)), where it is labeled *Pterophyllum matauriensis* (Mataura Falls). Apparently this was the only time Hector used this binomial (Thompson, 1913). When E.A.N.Arber (1917) described and figured *Pterophyllum matauriensis* Hector (op.cit.p.52; Pl.IX, Fig.2; Pl.XII, Fig.1) from Mataura Falls, he used Hector's 1886b sketch as the basis for the epithet and commented "Hector's figure ... is quite inaccurate as regards the apical characters of the leaflets, which are shown as if they were extremely acute, whereas in reality they are bluntly rounded."

Earlier, Hector (1878, 1879, 1880, 1886a) had applied the name *Palaeozamia matauriensis* to fossils from Flag Hill Series (Ben Bolt: see Mildenhall, 1970), Hokonui Hills, Waikawa, Mataura and Clent Hills, *Pterophyllum grandis* to fossils from Waikawa (1880) and Clent Hills (1886a), and *Cycadites pakawau* (1880) to fossils presumably from Pakawau. It seems most likely that Hector, in error, applied the name *Pterophyllum matauriensis* instead of *Palaeozamia matauriensis* to his published sketch (see above), and that the sketch actually represents the leaf type attributed by Arber to *Ptilophyllum acutifolium*. Indeed all the other *nomina nuda* given below can be readily equated with the two bennettite species described by Arber from the Jurassic of South Island, New Zealand.

Ettingshausen (1887, 1891) recognised two forms of pinnate cycadophyte from Mataura and Waikawa naming them *Pterophyllum dieffenbachii* and *Zamites mataurensis*, both *nomina nuda*. Crie (1888) gave the name *Zamites etheridgei* n.n. to fossils from Mataura.

Arber (1917) also described *Cycadites* sp., pinnule of a Cycadophyte, stem of (?)*Ptilophyllum*, *Nilssonia elegans* Arber and *Nilssonia compta?* (Phillips) Arber. Only the last named is considered further here. *N.elegans* is considered in Chapter 5.

Edwards (1934) supported Arber's determination of *N.compta* and *P.acutifolium*. He discussed the possibility of transferring *Pterophyllum "matauriense"* to *Nilssonia* and of uniting *N.elegans* with *N.schaumburgensis* (Dunker). Edwards also described (loc.cit.p.99) leaves collected by D.G.Lillie during 1910-1913 not dealt with by Arber as having "much more obtuse pinnules [than *Ptilophyllum acutifolium*], though both may belong to the same species". He states (loc.cit.) that "one specimen ([BMNH] V15783 Pl.V, Fig.2) of a pinna-base with broadly rounded pinnules, becoming slightly falcate above, can only be regarded as an *Otozamites*". However the criteria for separating *Otozamites* from *Ptilophyllum* given by Harris (1969,p.11) do not support such determination and the record of *Otozamites* in the Jurassic of New Zealand should be regarded with suspicion until further evidence is produced.

Oliver (1950) discussed and figured *Nilssonia elegans* (Pl.1, Fig.8), *Ptilophyllum "acutilobum"* (Pl.1, Fig.9) and *Pterophyllum "matauraensis"* (Pl.1, Fig.10) and discussed *N.compta* (p.4). The misuse of the specific epithet for the *Ptilophyllum* probably arose from an apparent typesetting error in Arber (1917) where "*Ptilophyllum acutilobum*" appears in the legend to Plate XI instead of *P.acutifolium*, probably as the result of confusion with *Dictyophyllum acutilobum* in the legend to Plate XII. Oliver (1955) further compounded the error by referring to *Pterophyllum antilobum* n.n. (see Mildenhall, 1970).

Raine (1982a), reporting on material held by the British Museum (Natural History) and the Sedgwick Museum, Cambridge, which had been considered by Arber, records *Pterophyllum* sp. cf.*Encephalartites* Vakhrameev from Clent Hills, *Nilssonia compta?* and a "pinnule of a Cycadophyte" from Mokoia, and *Pterophyllum matauriensis* from Malvern Hills "grey matrix".

Systematics

Class Cycadopsida

? *Nilssonia compta* (Phillips) Brongniart

New Zealand synonymy:

1917 *N.compta*? (Phillips): Arber 1917, p.51, Pl.VIII, Figs.2,3,9 (description and figures) (Mokoia).

1934 *N.compta* (Phillips): Edwards 1934, p.98, Pl.V, Fig.1 (figure only) (Waikawa).

1950 *N.compta* (Phillips): Oliver 1950, p.4 (brief description) (Waikawa).

Diagnosis: as given by Arber, 1917.

Discussion: Arber doubtfully attributed the Mokoia (Jurassic) fossils to the Yorkshire species. However, Edwards (1934) seemed in no doubt about referring the specimens collected by D.G.Lillie from Waikawa to *N.compta* and remarked (loc.cit.p.98) "the Mokoia and Waikawa specimens are certainly closely related". Harris (1964, p.54) points out that "Many specimens figured from other floras look more or less like *N.compta* and *N.kendalli*, but where fine details have been described there are differences. The question whether such specimens, whether determined as *N.compta* or given other names, are identical with the Yorkshire *N.compta* must be left until they are re-examined". His comment certainly applies to the New Zealand fossils identified as *N.compta*, and indeed is the reason for describing *N.pseudocompta* sp.nov. in Chapter 6. With regard to the New Zealand Jurassic fossils, it is probable that retention of Arber's query is the wisest course until further collection provides sufficient material to determine their true identity.

The occurrence in New Zealand of apparently but a single pinnate cycad species in both the Jurassic and the Cretaceous suggests that the fossils reported by Arber and Edwards are likely to be the ancestors of *N.pseudocompta* sp.nov.

Occurrence and Age: Mokoia, Waikawa; Temaikan, Middle Jurassic.

Order Bennettitales

Ptilophyllum acutifolium Morris

New Zealand synonymy:

1873 unnamed: Hector unpublished plates Pl.VII, Figs.14,15 plus five unnumbered figures (Mataura Falls).

1878 *Palaeozamia matauriensis*: Hector (name only)(Mataura Falls).

1886a *P.matauriensis*: Hector p.32 (name only) (Mataura Falls).

1886b *Pterophyllum matauriensis*: Hector p.66, Fig.30A(7) (figure only) (Mataura Falls).

1887 *Zamites mataurensis*: Ettingshausen p.367 (name only) (Mataura and Waikawa)[Thompson 1913, p.48 "C.M.; chirotypes, Mataura, 1"].

1888 *Z.etheridgei*: Crie (name only; paper not seen; see Mildenhall, 1970).

1917 *Ptilophyllum acutifolium* Morris: Arber, p.53, Pl.XI, Figs.1,2,5 (diagnosis and figures) (Waikawa).

1950 *P.acutilobum* Morr.: Oliver, p.4, Pl.I, Fig.9 (Brief description and figure, source unknown) (Waikawa).

1955 *Pterophyllum antilobum*: Oliver (paper not seen; see Mildenhall, 1970).

Diagnosis: as given by Arber, 1917.

Remarks: it seems certain that only one species of *Ptilophyllum* has been discovered in the N.Z. Jurassic unless a fossil which matches Oliver's 1950 sketch can be found. Only one N.Z. Cretaceous *Ptilophyllum* is so far known (see Chapter 6) and its pinna shape is quite different.

Occurrence and Age: Mataura Falls, Waikawa; Temaikan, Middle Jurassic.

Pterophyllum matauriensis Hector ex Arber.

New Zealand Synonymy:

1873 unnamed: Hector unpublished plates Pl.VII, Figs.16,17(no name or description)(Mataura Falls).

1880 *P.grandis*: Hector (name only; paper not seen)(Waikawa and Clent Hills).

1886a *P.grandis*: Hector p.32 (name only)(Clent Hills).

1886b *P.matauriensis*: Hector p.66 (wrong name to wrong diagram).

1887 *P.dieffenbachii*: Ettingshausen p.367 (name only) (Mataura and Waikawa).

1888 *P.dieffenbachii*: Crie p.104 (name only; paper not seen) (Mataura).

1917 *P.matauriensis* Hector: Arber p.52, Pl.IX, Fig.2; Pl.XII, Fig.1 (description and figures) (Mataura Falls).

1934 *P.matauriense* Hector: Edwards p.99 (no description or figure) (Mataura).

1950 *P.matauraensis* Hector: Oliver p.4, Pl.I, Fig.10 (brief description and inaccurate figure from Arber Pl.XII, Fig.1).

Holotype: B 64.8 (N.Z.G.S. collection) (Arber, Pl.IX, Fig.2).

?Syntype: V 11657, B.M.N.H. (Arber, Pl.XII, Fig.1).

N.B. Thomson 1913, p.47 states "D.M.; holotype and paratypes. C.M.; 1 specimen, Mataura (paratype of Hector)".

Diagnosis as given by Arber, 1917.

Occurrence and Age: Clent Hills, Mataura, Mataura Falls, Waikawa; Temaikan, Middle Jurassic.

2.3. Ginkgoalean Taxa

Ettingshausen (1887,1891) described *Ginkgocladus novae-zeelandiae* from the Late Cretaceous rocks at Wangapeka, Nelson and came "to the conclusion that this fossil could only belong to the *Taxineae*, which carry phyllodia, and [is] midway between *Phyllocladus* and *Ginkgo*" (Ettingshausen 1891, p.293). He describes it as being petiolate with a primary vein subtending secondary and tertiary veins which run to the apical margin without further bifurcation. Florin (1940, p.47) suggests it is "based on phylloclads of the genus *Phyllocladus*", and discounts any ginkgoalean affiliations. Gregg (1975) states that the holotype has not been found.

Bell (1956), under the order Ginkgoales, described a Triassic fossil from Black Jacks near Benmore Dam, South Canterbury as *Ginkgo digitata* (Brongniart) Heer. It, together with *Chiropteris biloba* Bell and *Chiropteris waitakiensis* Bell, was transferred by Retallack (1980) to *Ginkgophytopsis lacerata* which is considered by him incertae sedis. He also recorded the occurrence of *G.lacerata* at Tank Gully, Long Gully, near Highfield, Lake Gunn and Taylor's Creek, all New Zealand Triassic localities. Retallack (1983) later reported the occurrence of two further species of the same genus from Black Jacks, *G.cuneata* and *G.tasmanica*. All three species have anastomosing veins.

Retallack (1980), under the order Ginkgoales, described *Sphenobaiera robusta* (Arber) Florin from Tank Gully. He comments (loc.cit.p.40) "These leaves are relatively narrow and cuneate. Usually two deep divisions of the lamina extend from the apex down to the same level at about one half the length of the leaf. Thus there is a long undivided leaf base". It has dichotomising veins. *S.robusta* also occurs at Long Gully (Retallack, 1981) together with *Karkeniania fecunda* Retallack, a ginkgoalean ovulate cone.

Appendix 3

Computational Data

3.1 *Phyllopteroides* Data

Character States:

- 1 Margin; 1 = biserrate, 2 = serrate, 3 = dentate, 4 = entire.
- 2 Pinna width: in mm.
- 3 Pinna shape; 1 = elliptic, 2 = ovate, 3 = oblanceolate, 4 = lanceolate; 5 = oblong.
- 4 Veins per tooth; 1 = 1 per tooth, 2 = 1 & 2 per tooth, 3 = 2 per tooth,
4 = 2 & 3 per tooth;, 5 = 2-4 per tooth.
- 5 Maximum tooth size; in 0.1 mm.
- 6 Tooth density; number per 10 mm.
- 7 Vein density; number per 10 mm.
- 8 Vein angle; in degrees.

Database:

Format Statement: 1I1,1I2,2I1,4I2.

OTU	Fossil No.	Data (N.B. 7 = No Comparison.)
1	220.08b1	2131103202466
2	220.09b(1)#1	1151205182265
3	220.09b(1)#2	2111102071858
4	220.12a(2)	2181304101864
5	220.14b	2151305122065
6	220.15	1151303121859
7	220.17b	1151105242666
8	220.18	1201218121864
9	220.19a	1131103202073
10	220.22	1161305122051
11	214.06b(2)	1251110101268
12	214.10a	1155205141855
13	214.13b(1)	1181206121861
14	750.17#1	2152706071667

15	750.17#2	2144105091276
16	750.17#3	2142107071850
17	750.17#4	2122105121247
18	750.17#5	2202210081870
19	750.17#6	2102202151665
20	411.08/22#1	4104707071243
21	411.08/22#2	4124707071440
22	411.20#1	3101402113064
23	411.20#2	4107707071245
24	412.45	4103707071438
25	412.47	3201525061835

3.2 Taeniopterid Data

Character States:

- 1 Pinna Width; in cm.
- 2 Midrib Width; in cm.
- 3 Minimum angle of secondary veins; in degrees.
4. Maximum angle of secondary veins; in degrees.
- 5 Ratio of midrib width over pinna width.
- 6 Maximum angle minus minimum angle.

Database:

Format Statement: F3.2,F2.2,2I2, . F3.3,I2.

OTU	Fossil No.	Data (N.B. 7 = No Comparison.)
1	100.06	12012808010000
2	100.08	21007658003015
3	100.25	05010707020000
4	121.15	20020656510000
5	121.15	23013606506005
6	121.15	25015606506005
7	123.01	17015658008015
8	123.02	20015708007510
9	123.02	15020656513000

10	123.02	13012657009005
11	123.02	12014707012000
12	123.03	15012303508005
13	123.04	24025656510000
14	123.04	25025658010015
15	123.05	12012657010005
16	123.06	20010656505000
17	123.07	18010656505000
18	123.08	12025606520005
19	123.10	26015606506005
20	123.16	14014708010010
21	123.22	12010808008000
22	613.23	16510658007815
23	613.39	16519658011115
24	613.40	10013808013000
25	613.41	12015659012525
26	613.42	17017677310007
27	732.21	12015659012525
28	330.14	25015808006000
29	330.14	15008808005000
30	330.14	20015708007510
31	330.14	20012808006000
32	330.14	24015708006310
33	330.14	20013808006500
34	330.16	15013758009005
35	330.16	18010657006005
36	330.16	16015808009000
37	411.05	11013808012000
38	732.15	15010658007015
39	740.02	09010909011000
40	742.01	13010708008010
41	742.03	18012709007020
42	742.06	12010659008025
43	742.13	12020808016000
44	742.13	16010658006315
45	742.13	10017809017010
46	742.19	12008658007015
47	742.19	12012659010025

48	742.31	15010809007010
49	742.31	12010659008025
50	742.39	15010658007015
51	742.43	20010769005014
52	742.50	13020659015025
53	742.50	12012656510000
54	100.03	09010656511000
55	100.05	24020808008000
56	100.12	12018656515000
57	100.15	21020708009010
58	100.17	15022808015000
59	100.29	20020708010010
60	300.31	17010708006010
61	300.36	12007677604008
62	300.40	07007697606007
63	310.12	17010737614003
64	310.13	20010708006010
65	310.13	30015808007500
66	310.31	20022708007010
67	330.05	18016658008015
68	330.05	09014658008015
69	330.06	20010708011010
70	330.16	08515707007500
71	412.20	35015909017000
72	522.51	20015657004005
73	712.21	16014728009008
74	742.28	20008454504000
75	750.01	16012808007500
76	220.08a	15010657307008
77	732.03	05010 200
78	732.17	04005 125
79	732.20	03005 166
80	732.25	04510 222
81	732.28	02510 400
82	732.43	04510 222
83	732.45	04510 222
84	732.46	04505 111
85	732.52	04510 222

86	732.61	02005	250
87	732.67	04505	111
88	742.02	04512	266
89	742.03	07512	160

3.3 *Araucaria* and *Agathis* Data (35 characters)

Character	Character states:
1 Leaf length maximum	cm.
2 Leaf length minimum	cm.
3 Leaf width maximum	cm.
4 Leaf width minimum	cm.
5 Petiole	0 = present, 1 = absent.
6 Cuticle thickness	1 = thin, 2 = medium, 3 = thick.
7 Adaxial cell shape	1 = isodiametric, 2 = mixed, 3 = rectangular.
8 Adaxial cell length St.Dev.	continuous.
9 Adaxial cell length mean	um.
10 Adaxial cell width St.Dev.	continuous.
11 Adaxial cell width mean	um.
12 Adaxial cell arrangement	1 = mixed, 2 = tetragonal, 3 = pentagonal, 4 = hexagonal, 5 = linear oblique.
13 Adaxial anticlinal cell wall pattern	1 = straight, 2 = rounded, 3 = undulate.
14 Adaxial anticlinal cell wall ornament	1 = absent, 2 = knobs, 3 = ridges, 4 = T thickening, 5 = pitted.
15 Adaxial cell alignment (between stomatal bands)	1 = random, 2 = poorly aligned, 3 = well aligned.
16 Abaxial cell shape	1 = isodiametric, 2 = mixed, 3 = rectangular.
17 Abaxial cell length St.Dev.	continuous.
18 Abaxial cell length mean	um.
19 Abaxial cell width St.Dev.	continuous.
20 Abaxial cell width mean	um.
21 Abaxial cell arrangement	1 = mixed, 2 = tetragonal, 3 = pentagonal, 4 = hexagonal, 5 = linear oblique.

- | | | |
|----|---|---|
| 22 | Abaxial anticlinal cell wall pattern | 1 = straight, 2 = rounded, 3 = undulate. |
| 23 | Abaxial anticlinal cell wall ornament | 1 = absent, 2 = knobs, 3 = ridges,
4 = T thickening, 5 = pitted. |
| 24 | Abaxial cell alignment (between stomatal bands) | 1 = random, 2 = poorly aligned,
3 = well aligned. |
| 25 | Stomatal location | 1 = upper many, lower many, 2 = upper few, lower many,
3 = upper none, lower many. |
| 26 | Stomatal orientation | 1 = parallel to veins, 2 = oblique,
3 = perpendicular to veins. |
| 27 | Stomatal Index
$I = (S/(S+E)) \times 100$ | continuous |
| 28 | Number of stomatal files per band | continuous |
| 29 | Number of files of cells in interstomatal bands | continuous |
| 30 | Number of subsidiary cells | 1 = 4, 2 = 4-5, 3 = 4-6 |
| 31 | Arrangement of subsidiary cells | 0 = only paratetracytic,
1 = paratetracytic and staurocytic |
| 32 | External opening shape | 1 = circular, 2 = oval, 3 = elongated |
| 33 | External opening prominence | 1 = flat, 2 = prominent, 3 = very prominent |
| 34 | External visibility of anticlinal cell wall | 1 = not visible, 2 = slightly visible, 3 = prominent |
| 35 | External arrangement of stomata in rows | 1 = random, 2 = irregular rows, 3 = regular rows |

OTUs with Whitmore's synonymy in brackets, herbarium number, native country and source of specimen (if different).

- | | | |
|---|--|---|
| 1 | <i>Araucaria araucana</i> (Molina) K.Koch; | Chile, N.Z. <i>cultivated</i> . |
| 2 | <i>A. angustifolia</i> (Bertol.) O.Kuntze; | Brazil, N.Z. <i>cultivated</i> |
| 3 | <i>Agathis australis</i> (Lambert) Steud., | CANU, N.Z. |
| 4 | <i>A. brownii</i> Hort. ex Lemaire; (sp. dub.) | CHR85005A, New Caledonia?, N.Z. <i>cultivated</i> . |
| 5 | <i>A. lanceolata</i> Lindley ex Warburg; | CHR407437, New Caledonia. |
| 6 | <i>A. sp. indet.</i> "Mt. Mou"; | CANU, from Mt. Mou, New Caledonia. |
| 7 | <i>A. sp. indet.</i> "R. Bleue"; | CANU, from R. Bleue, New Caledonia. |
| 8 | <i>A. macrophylla</i> (Lindley) Masters; | CHR409318A, Melanesia, W. Samoa <i>cultivated</i> . |

- 9 *A.obtusa* (Lindley) Masters;(*A.macrophylla*) CHR298892, Melanesia,
New Hebrides ex Herbario Kewensi.
- 10 *A.ovata* (C.Moore ex Vieillard) Warburg; CHR407440, New Caledonia.
- 11 *A.palmerstonii* (F.Muell.)F.M.Bailey;(*A.robusta* subsp.*robusta*) CHR219564, Queensland, N.Z.
- 12 *A.robusta*? (C.Moore ex F.Muell.)F.M.Bailey; CHR35700, Queensland.
- 13 *A.vitiensis*"N"(Seeman)Benth.& Hook.f.;(*A.macrophylla*) CHR15270, Melanesia,
Nausori Highlands of Fiji.
- 14 *A.vitiensis*"F"(Seeman)Benth.& Hook.f.;(*A.macrophylla*) CHR65353, Melanesia, lowlands of
Fiji.
- 15 *A.seymouricum* sp.nov.; CU700.05Cl, N.Z.

Database:

Format Statement: F3.1,F2.1,2F3.2,3I1,F3.2,F4.2,F3.2,F4.2,5I1,F3.2,F4.2,F3.2,F4.2,
3I1,3I1,F3.1,8I1.

OTU Data (N.B. 7 = No Comparison).

1 0353012010003314253600281790533321986500056176012331109315102113

2 0301507006003317268800421330515331516980041138051531114915303113

3 0604012009002110138300793760121321226290059209012122213613211321

4 1201025010003114238750472425124321664800120257511113320513212322

5 0955522512501107727500522075114221494350070247511223222322213333

6 1006017010002226985500432125511221807825050230012123313313102223

7 0957520010002117462500762500114222556225053272512123212112111333

8 1309040020011220765000983525122332357450143357512523313814101313

9 0855522515003108228000442250314110983650048198012213310912213333

10 0574525015003110331500793125124111213625066202512433324222212333

11 1158520010013109335000552475124211263475068260011112312413211312

12 1207035020012108938500502750134221324025073232513313314222213223

13 0605015010012106930770442325111121443675067187511133315732102232

14 0804030015011219577500814000231324377475064347511133314313102332

15 0552012005002135822452351964421324113816115233012132307013212772

3.4 Fossil *Agathis* Data (13 Characters)

Character States:

- 1 Maximum leaf length; in cm.
- 2 Minimum leaf length; in cm.
- 3 Maximum leaf width; in cm.
- 4 Minimum leaf width; in cm.
- 5 Adaxial anticlinal cell wall pattern; 0 = straight, 1 = not straight.
- 6 Adaxial anticlinal cell wall ornament; 0 = absent, 1 = present.
- 7 Adaxial cell alignment; 0 = poorly aligned, 1 = well aligned.
- 8 Abaxial anticlinal cell wall pattern; 0 = straight, 1 = not straight.
- 9 Abaxial cell alignment; 0 = poorly aligned, 1 = well aligned.
- 10 Stomatal frequency on adaxial surface; 1 = none, 2 = few, 3 = many.
- 11 Stomatal orientation; 0 = random, 1 = transverse.
- 12 Number of subsidiary cells; 0 = 4 or 5, 1 = 4, 5 or 6.
- 13 Stomatal arrangement in rows; 1 = random, 2 = irregular, 3 = regular.

OTUs:

- 1 *Agathis australis* from Cookson and Duigan 1951.
- 2 *A. australis* from present study.
- 3 *A. seymouricum* sp.nov.
- 4 *A. parwanensis* from Cookson and Duigan 1951.
- 5 *A. yallournensis* from Cookson and Duigan 1951.
- 6 *A. clarencianum* sp.nov.

Database:

Format Statement; F3.1,3F2.1,9I1.

OTU Data (N.B. 7 = No Comparison)

1	050152010111772012
2	070401506101102001
3	055201205101113102
4	070701070011011102
5	095702010010012013
6	130451804001011103

3.5 Fossil *Agathis* Data (32 characters).

Character	Character states:
1 Leaf length maximum	cm.
2 Leaf length minimum	cm.
3 Leaf width maximum	cm.
4 Leaf width minimum	cm.
5 Veins	0 = obvious, 1 = not obvious.
6 Leaf shape	1 = ovate, 2 = ovate-lanceolate, 3 = lanceolate, 4 = oblanceolate.
7 Adaxial cell shape	1 = isodiametric, 2 = mixed, 3 = rectangular.
8 Adaxial cell length St.Dev.	continuous.
9 Adaxial cell length mean	um.
10 Adaxial cell width St.Dev.	continuous.
11 Adaxial cell width mean	um.
12 Adaxial cell arrangement	1 = mixed, 2 = tetragonal, 3 = pentagonal, 4 = hexagonal, 5 = linear oblique.
13 Adaxial anticlinal cell wall pattern	1 = straight, 2 = rounded, 3 = undulate.
14 Adaxial anticlinal cell wall ornament	1 = absent, 2 = knobs, 3 = ridges, 4 = T thickening, 5 = pitted.
15 Adaxial cell alignment (between stomatal bands)	1 = random, 2 = poorly aligned, 3 = well aligned.
16 Abaxial cell shape	1 = isodiametric, 2 = mixed, 3 = rectangular.
17 Abaxial cell length St.Dev.	continuous.

18	Abaxial cell length mean	um.
19	Abaxial cell width St.Dev.	continuous.
20	Abaxial cell width mean	um.
21	Abaxial cell arrangement	1 = mixed, 2 = tetragonal, 3 = pentagonal, 4 = hexagonal, 5 = linear oblique.
22	Abaxial anticlinal cell wall pattern	1 = straight, 2 = rounded, 3 = undulate.
23	Abaxial anticlinal cell wall ornament	1 = absent, 2 = knobs, 3 = ridges, 4 = T thickening, 5 = pitted.
24	Abaxial cell alignment (between stomatal bands)	1 = random, 2 = poorly aligned, 3 = well aligned.
25	Stomatal location	1 = upper many, lower many, 2 = upper few, lower many, 3 = upper none, lower many.
26	Stomatal orientation	1 = parallel to veins, 2 = oblique, 3 = perpendicular to veins.
27	Stomatal Index $I = (S/(S+E)) \times 100$	continuous
28	Maximum number of stomatal files per band	continuous
29	Number of files of cells in interstomatal bands	continuous
30	Number of subsidiary cells	1 = 4, 2 = 4-5, 3 = 4-6
31	Arrangement of subsidiary cells	0 = only paratetracytic, 1 = paratetracytic and staurocytic
32	External arrangement of stomata in rows	1 = random, 2 = irregular rows, 3 = regular rows

OTUs:

- 1 *Agathis australis* from present study.
- 2 *A.seymouricum* sp.nov.
- 3 *A.clarencianum* sp.nov.
- 4 *A.parwanensis* from Cookson and Duigan 1951.
- 5 *A.yallournensis* from Cookson and Duigan 1951.
- 6 *A.robusta* from present study.

Database:

Format Statement: F3.1,3F2.1,3I1,F3.2,F4.2,F3.2,F4.2,5I1,
F3.2,F4.2,F3.2,F4.2,6I1,F3.1,5I1.

OTU Data

1	07040150602110138300793760121321226290059209012122213613211
2	05520120501135822452351964421324113813115233012131306713212
3	13045180414214249750572475111321826286051226021133316649103
4	08080108018218254500603125215322346300146332521533312823302
5	09535201013113543751083650315232426375125265021532214336313
6	12070351503108938500502750134221324025073232513313314222213

3.6 Dicotyledonous Leaf Data (16 characters)

Character States:

- 1 Length of lamina; in mm.
- 2 Maximum lamina width; in mm.
- 3 Distance from point of petiole insertion to widest point of lamina
 measured along the midrib; in mm.
- 4 Basal angle; in degrees.
- 5 Apical angle; in degrees
- 6 Minimum secondary vein angle; in degrees.
- 7 Maximum secondary vein angle; in degrees.
- 8 Lamina shape as described by the ratio length/width (L/W).
- 9 Lamina shape as described by the ratio length/ base to widest point (L/BTOW).
- 10 Secondary vein type; 1 = simple, 2 = simple/semicraspedodromous,
 3 = semicraspedodromous, 4 = eucamptodromous/simple,
 5 = eucamptodromous, 6 = eucamptodromous/cladodromous, 7 = cladodromous,
 8 = eucamptodromous/brochidodromous, 9 = brochidodromous.
- 11 Secondary vein branching; 1 = none, 2 = lower only, 3 = upper and lower, 4 = equal.
- 12 Secondary vein course; 1 = straight, 2 = sinuous or zigzag.
- 13 Secondary vein curvature; 1 = straight, 2 = abrupt, 3 = uniform.
- 14 Margin; 1 = entire, 2 = slightly wavy, 3 = wavy, 4 = erose.
- 15 Marginal glands which are here determined as hydathodes; 1 = absent, 2 = present.
- 16 Lowest pair of secondary veins weak, more acute; 1 = absent, 2 = present.

Database:

Format Statement; F3.1,2F2.0,2F3.0,2F2.0,2F2.1,7F1.0.

OTU	Fossil No.	Data
[reduced set]	(* numerotype)	(Computed estimates underlined.) (9 = No Comparison.)
1	[1] 100.03#2	0753330109069575723253222121
2	[2] 100.03#4	1053945132039555527233222111
3	[3] 100.04#10/05#8	0732733105047345427222222111
4	[4] 100.04#12/34#4	08131381000 <u>045616126213223111</u>
5	[5] 100.04#13	<u>086353510904552525232222111</u>
6	[6] 100.07#1	<u>0863537115045565625235222122</u>
7	[7] 100.08#5	<u>0864240116045474725232222111</u>
8	[8] 100.08#19	0833635138040616123243222111
9	[9] 100.10#1	1103838134042494929297222111
10	[10] 100.14#2/17#14	1454650116028545432292222121
11	[11] 100.14#4/#8	09436421 <u>17042535326223223111</u>
12	[12] 100.14#6/17#14	1154450139043595926232222191
13	[13] 100.16#2*	0853437119045575725232222111
14	[14] 100.17#10	<u>0864035115045585825232222111</u>
15	[15] 100.19	0733030100054505024242222121
16	[16] 100.17#6	<u>0863437117049575725231223111</u>
17	[17] 100.17#13	<u>0863537117041525225231222191</u>
18	[18] 100.22#3	<u>0863537115045575725233222191</u>
19	[19] 100.24#2	<u>0865040127045505025232223111</u>
20	[20] 100.25#4	04530301370 <u>45565615157223121</u>
21	[21] 100.25#8	0602728115047565622217226121
22	[22] 100.27	<u>0863637117044484825233222121</u>
23	[23] 100.31	<u>0863740124045595925231223111</u>
24	[24] 310.22	0602530097044 <u>555524203222191</u>
25	[25] 310.27	<u>0862830094045656525232223191</u>
26	[26] 310.34	<u>0603245064078606822177221121</u>
27	[27] 412.34	<u>0603023061078346422173221191</u>
28	[28] 522.56	<u>0604040073078385122177221121</u>
29	[29] 522.72#1	<u>0602015066078355222171221121</u>

30	[30]	522.72#2 [*]	0602735061078406522171221121
31	[31]	522.73#2	<u>0603035058078404022171221121</u>
32	[32]	522.61#8	<u>0603032078078516022171211191</u>
33	[33]	330.43#1	<u>1203137047050365030241221192</u>
34		522.61#6	<u>1201635070050383830248212112</u>
35	[34]	522.73#1 [*]	1204050061050365030241221112
36	[35]	742.17	<u>1203537050050375730241221192</u>
37	[36]	742.21#1	<u>1203025081050617230241221112</u>
38	[37]	742.21#2	<u>1203240079050476330245221192</u>
39		410.01 [*]	0751639047031335747199222122
40		411.41 [*]	0752233070096335034239222121
41		100.12b#1 [*]	0603535142120525217178213121
42	[38]	100.22#2	0552520112057555522288223111
43		100.25#2	<u>0574035165120474719235213121</u>
44	[39]	100.01#6	0702725083038585826285112121
45	[40]	100.03#3	0552322120043595924257212121
46	[41]	100.03#5	<u>0882233120043545426273212111</u>
47	[42]	100.03#9/05#7	<u>0883432121040606026275112121</u>
48	[43]	100.03#14/34#5	<u>0883233117040565626279212121</u>
49	[44]	100.07#3	<u>0883233120041525226275112121</u>
50	[45]	100.08#7 [*]	0953537124036505027265212121
51	[46]	100.08#10	1274542125038464628305112121
52	[47]	100.08#17	0954040150040535324245112121
53	[48]	100.032	<u>0883233120039545426275212121</u>
54	[49]	310.38	<u>0883233120040676726275213121</u>
55	[50]	100.01#4	0973640075057575727246222122
56	[51]	100.03#7/34#3 [*]	1003338084038606030265222112
57	[52]	100.05#5	<u>0713640071039585890905222122</u>
58	[53]	100.05#6	0651925090039555534265222121
59	[54]	100.08#9	0802438052036484833216222121
60	[55]	100.08#13	<u>0713134116043595927226222122</u>
61	[56]	100.08#15	<u>0712934098043444427224223122</u>
62	[57]	100.0816	<u>0713033090043555527225222122</u>
63	[58]	100.08#20	<u>0712834085043555527225222122</u>
64	[59]	100.07#2	<u>0712734085043484827225222122</u>
65		100.14#14	<u>0712934084043555527227223121</u>
66		100.17#12	0903045118043484890907223121
67	[60]	100.17a#12b	<u>0712934086043525227225222122</u>

68	[61]	100.21#3	<u>0712934085043606027225222122</u>
69	[62]	100.25#1	0381618061044464624215222112
70	[63]	100.25#3	<u>0714825080043505027223222122</u>
71	[64]	100.26#1	<u>0712934087043585827225222122</u>
72	[65]	123.17	<u>0713337082043595927226222122</u>
73	[66]	522.62#2	<u>0712034085033676727228222122</u>
74	[67]	522.62#3	<u>0712534085051414127228222122</u>
75	[68]	522.62#9	0582425093409535324235222122
76	[69]	613.22	<u>0713434085043535327225222122</u>
77	[70]	613.18	<u>0713340073043424227225223122</u>
78	[71]	100.12#3	0622535076045525225185223121
79	[72]	100.13#3	<u>0852625082042525228216223991</u>
80	[73]	100.14#9 *	1083645086032535330246223221
81	[74]	123.12#2	<u>0852329080040656528216223121</u>
82	[75]	522.62#1	<u>0852225082040707028215223121</u>
83	[76]	100.01#1	1103344089023595933257423221
84	[77]	100.03#6	<u>1204147092029444431277423221</u>
85	[78]	100.03#11	<u>1204147092030616131277423111</u>
86	[79]	100.03#15	<u>1204447092029575731277423211</u>
87	[80]	100.05#2	<u>1204150100029585831277422211</u>
88	[81]	100.05#3	<u>1203547092040595931277423211</u>
89	[82]	100.08#2	1063350070030595932217423211
90	[83]	100.08#14	<u>1203043101029646431277423121</u>
91	[84]	100.10#2/09	1303847103026484834287423121
92	[85]	100.13#1	<u>1205247077030656531277423211</u>
93	[86]	100.13#2	<u>1204247092029484831277122211</u>
94	[87]	100.14#3/17#14b	1234545093026686827277423221
95	[88]	100.14#12	<u>1204647092029676731277423211</u>
96	[89]	100.14#13	<u>1204245104032656531277423211</u>
97	[90]	100.14#15/08	1104242093021595926261123211
98	[91]	100.17#2 *	1404442100028575732337423211
99	[92]	100.23	<u>1204147092037565631277423211</u>
100	[93]	121.11	<u>1204447092022626231277423211</u>
101	[94]	220.16	<u>1204047092034505031277423311</u>
102	[95]	330.42#1	<u>1205265092029656531277423311</u>

3.7 Dicotyledonous Leaf Holotype Data (30 characters)

Character States:

- 1 Maximum length of midrib (L) of the longest leaf, complete or incomplete, from each form species; in mm.
 - 2 Maximum lamina width (W) of holotype; in mm.
 - 3 Distance from base to widest point of lamina measured along midrib (BTOW) of holotype.
 - 4 Basal angle of holotype; in degrees.
 - 5 Apical angle of holotype; in degrees.
 - 6 Lamina shape as described by the ratio length/width (L/W).
 - 7 Lamina shape as described by the ratio length/ base to widest point (L/BTOW).
 - 8 Area; 1 = microphyll, 2 = notophyll, 3 = *mesophyll*.
-
- 9 Lamina Form; 1 = narrow oblong, 2 = oblong, 3 = narrow obovate, 4 = wide obovate, 5 = narrow elliptic, 6 = elliptic, 7 = elliptic/narrow ovate, 8 = narrow elliptic/lanceolate, 9 = lanceolate, 10 = narrow ovate, 11 = ovate, 12 = very wide obovate.
 - 10 Lamina Balance; 1 = symmetrical, 2 = asymmetrical.
 - 11 Basal balance; 1 = symmetrical, 2 = slightly asymmetrical, 3 = asymmetrical, 4 = very asymmetrical.
 - 12 Base shape; 1 = decurrent, 2 = cuneate, 3 = normal.
 - 13 Apex Shape; 1 = attenuate, 2 = acute, 3 = rounded, 4 = obtuse, 5 = emarginate.
 - 14 Margin; 1 = entire, 2 = slightly crenate, 3 = coarsely crenate, 4 = lobed, 5 = obtuse serrate, 6 = acutely serrate.
Combinations are coded as means e.g. entire/slightly crenate = 1.5.
 - 15 Marginal glands (hydathodes); 1 = absent, 2 = present.
 - 16 Lamina texture; 1 = very membranaceous, 2 = membranaceous, 3 = chartaceous.
 - 17 Secondary vein type; 1 = simple, 2 = semicraspedodromous, 3 = cladodromous, 4 = eucamptodromous, 5 = brochidodromous.
 - 18 Secondary vein angle variation; 1 = uniform, 2 = lowest pair more acute, 3 = more acute on one side, 4 = upper more obtuse,

- 5 = upper more acute, 6 = irregular.
- 19 Secondary vein thickness relative to primary vein thickness; 1 = fine, 2 = moderate, 3 = thick, 4 = very thick.
- 20 Secondary vein branching; 1 = none, 2 = lower only, 3 = upper and lower, 4 = equal.
- 21 Secondary vein course; 1 = straight, 2 = sinuous or zigzag.
- 20 Secondary vein curvature; 1 = straight, 2 = uniform curve, 3 = abrupt curve, 4 = increasing curvature up the leaf, 5 = upper curve up/ lower curve down, 6 = recurved.
- 23 Secondary vein arrangement; 1 = converging, 2 = approx. parallel, 3 = diverging.
- 24 Secondary vein maximum angle to midrib; in degrees.
- 25 Secondary vein loops join superadjacent vein; 1 = acutely, 2 = at right angles, 3 = do not loop.
- 26 Secondary vein loop enclosed by tertiary vein loops; 1 = not enclosed, 2 = enclosed.
- 27 Intersecondary veins; 1 = absent, 2 = simple, 3 = composite.
- 28 Tertiary vein angle of origin, exmedial side first;
1 = acute/acute, 2 = acute/right angle, 3 = right angle/acute, 4 = right angle/right angle, 5 = obtuse/right angle.
- 29 Tertiary vein pattern; 1 = random reticulate, 2 = orthogonal reticulate, 3 = percurrent.
- 30 Areoles; 1 = well developed, 2 = imperfect, 3 = incompletely closed, 4 = lacking.

Database:

Format Statement: F3.0,2F2.0,2F3.0,2F2.1,F1.0,F2.0,4F1.0,F2.1,9F1.0,F2.0,6F1.0.

OTU	Fossil No.	Data
		(Measurements from fossils other than holotype underlined)
		(9 = No Comparison)
1	100.16#2	145343711904525232071312102311222325731121 <u>2</u>
2	220.19	0934450076060211920213121021113114243311233
3	121.01	1104545095110202020613126021142214244311233
4	100.16#3	065232508704 <u>52826</u> 1061214501114422226631111 <u>2</u>
5	522.72#2	0652735061078221710321222013112221265311311
6	522.73#1	1204050061050302420922222023133226250313313
7	100.12#1	0603535142320171710423151013412222252223411
8	100.08#7	127353712403627262101311101241111325031121 <u>2</u>
9	100.03#7	1003338084038302620822111012411223260313213

10	100.14#9	1083645086032302420912111523313422257311212
11	100.17#2	1404442100028323330912111523313422257311212
12	100.01#2	0801920115048242311023122021311211259312421
13	212.08(1)#3	0351517080136211910623141513312421252311411
14	214.20	1336855160030202431014133023213423260223411
15	522.09	1103560080068311820511321022262422283223213
16	212.01	0703723174036172711012121011522212175221221
17	522.62#4	0501622045052322310111221011521216163221313
18	410.01(1)	0751639047031471910511121512541223157113321
19	122.08	1408066172040202131113123511153315348311233
20	220.12	1226252098035202320612223021113214355311233
21	411.41	0702233070096342310111141212511426150221522
22	214.19#2	0454835085323091311211151022443426267223411

Appendix 4

Locality, Site and Bed Data

Locality 0: Red Hill Creek.

Site 1: McKay's site S.W. of Red Hill, G.R.S41/793205.

Bed 2: bed 2 of McKay (1886).

Collection: I.L.Daniel and J.D.Lovis, 12 Feb.1986.

Locality 1: Horse Flat.

Site 0: loose boulders on river bank, G.R.S41/769169.

Bed 0: boulders not *in situ*.

Collection: J.D.Lovis, *et al.*, Dec.1978, Apr.1979.

Site 1: upstream from solitary willow, G.R.S41/764167

Bed 1: prominent mudstone bed.

Collection: I.L.Daniel and J.D.Lovis, 7 Feb.1985.

Site 2: downstream from solitary willow, G.R.S41/772170.

Bed 0: boulders not *in situ*.

Bed 1: boulders fallen from major crevasse splay.

Bed 2: muddy sandstone blocks.

Bed 3: stratigraphically lowest crevasse splay.

Collection: I.L.Daniel and J.D.Lovis, 7 Feb.1985,

15 Jan.1986, 13 Feb.1986.

Locality 2: Alexander McKay Terrace.

Site 1: S.E.end of terrace, G.R.S41/747152.

Bed 0: loose nodules in mudstone at foot of terrace.

Bed 2: small crevasse splay, first from S.E.end of terrace.

Bed 4: fourth crevasse splay from S.E.end.

Bed 5: sixth crevasse splay from S.E.end.

Bed 6: seventh crevasse splay from S.E.end.

Bed 7: twelfth crevasse splay from S.E.end.

Collection: I.L.Daniel and J.D.Lovis, 7 Feb.1985,

11-13 Feb.1986.

Site 2: loose boulders on old river bed at foot of terrace,

G.R.S41/746153.

Bed 0: boulders not *in situ*.

Collection: I.L.Daniel and J.D.Lovis, 12-13 Feb.1986.

Locality 3: East Quail Flat.

Site 0: west end of main outcrop at river level, G.R.S41/744146.

Bed 0: "*Eretmophyllum*" and "*Ginkgo*" horizons.

Collection: J.D.Lovis *et al.*, Dec.1978.

Site 1: old (high) road cutting midway between spurs,

G.R.S41/745144.

Bed 0: single boulder not *in situ*.

Collection: I.L.Daniel, 8 Mar.1984, 13 Dec.1984.

Bed 1: "*Eretmophyllum*" horizon just above road at west end of exposure.

Collection: I.L.Daniel and J.D.Lovis, 13 Dec.1984.

Site 2: new (low) road cutting, middle corner, G.R.S41/743144,

Bed 1: 15cm.thick "*Eretmophyllum*" bed immediately west of soak.

Bed 2: "*Ginkgo*" bed, three metres west of Bed 1.

Collection: I.L.Daniel and J.D.Lovis, 10,13 Dec.1984.

Site 3: beach downstream from outcrop on true right bank,

G.R.S41/747146.

Bed 0: boulders not *in situ*.

Collection: I.L.Daniel and J.D.Lovis, 10 Feb.86, 3,5 Feb. 1987.

Locality 4: West Quail Flat.

Site 1: halfway down bulldozed track, G.R.S41/727147.

Bed 0: boulders not *in situ*.

Bed 1: sandstone above volcanic tuff.

Bed 2: shaly mudstone below volcanic tuff.

Collection: J.D.Lovis *et al.*, Dec.1978;

I.L.Daniel and J.D.Lovis, 12 Dec.1984.

Site 2: downhill from top end of bulldozed track, G.R.S41/728148.

Bed 1: grits, sandstone and mudstone dipping steeply N.W.

Collection: I.L.Daniel and J.D.Lovis, 4 Feb.1988,

N.B. this is the only collection from the 1988 field season included in the thesis. It is included because it contains the only occurrence of *Otozamites*.

Locality 5: Ptilophyllum Ridge.

Site 1: cliffs at head of stream, G.R.S41/737120.

Bed 1: between basalt flows.

Collection: I.L.Daniel, 25 Nov.1983.

Site 2: ridge south of basalt, G.R.S41/734118.

Bed 1: ridge-point just above 2600 ft. contour.

Bed 2: north side of ridge, 50m. north of Bed 1.

Bed 3: loose boulder up gully north of Bed 2.

Collection: I.L.Daniel and J.D.Lovis, 16,17 Jan.1986,

11 Feb. 1986, 4 Feb. 1987.

Locality 6: Lower Seymour Stream.

Site 1: west bank, south of basalt, G.R.S41/726115.

Bed 0: boulders not *in situ*.

Beds 1-3: sandstone beds between coaly bed and basalt.

Beds 4-5: between Beds 2 and 3;

Bed 4, coaly lens in sandstone 2m. above Bed 2;

Bed 5, immediately below Bed 3.

Collection: I.L.Daniel and J.D.Lovis, 26 Nov.1983,

7 Mar.1984, 14 Jan.1986, 6 Feb.1987.

Site 2: alluvial fan on east bank, G.R.S41/727116.

Bed 0: boulders not *in situ*.

Collection: I.L.Daniel and J.D.Lovis, 16 Jan.1986.

Locality 7: Upper Seymour Stream.

Site 0: boulders on west bank of Seymour Stream, upstream
from basalt, G.R.S48/739074.

Bed 0: boulders not *in situ*, lithology similar to 712.

Collection: J.D.Lovis *et al.*, Dec.1978.

Site 1: coal measures on west bank of Seymour Stream,
upstream from basalt, G.R.S48/739074.

Bed 1: 20cm. thick fossiliferous bed 2m. below (south of)
lowest basalt flow.

Bed 2: muddy bed on top of tuff below Bed 1.

Bed 8: third sandstone bed below tuff.

Collection: I.L.Daniel and J.D.Lovis, 4 Feb.1985,
5 Dec. 1985, 14 Jan.1986, 6 Feb 1987.

Site 3: east bank of Black Rock Stream, upstream from basalt
G.R.S48/737073.

Bed 2: tuff opposite hut.

Collection: I.L.Daniel and J.D.Lovis, 6, 8 Feb.1985,
18 Jan.1986.

Site 4: east bank of Seymour Stream, stratigraphically below
(south of) lowest basalt flow, G.R.S48/741075.

Bed 0: boulders not *in situ*.

Bed 2: tuff with muddy and gritty lenses.

Bed 7: sandy mudstone.

Collection: I.L.Daniel and J.D.Lovis, 5 Feb.1985.

Site 5: east bank of Seymour Stream, stratigraphically below
(south of) Site 4, G.R.S48/741074.

Bed 0: boulders fallen from the northern of two slips.

Bed 1: sandstone exposed on northern side of northern slip.

Collection: I.L.Daniel and J.D.Lovis, 5,6 Feb.1985,
6 Feb. 1987.

Locality 8: Coal Creek.

Site 2: upstream end of coal measures, G.R.S48/742093.

Bed 0: boulders not *in situ*.

Collection: I.L.Daniel and J.D.Lovis, 18 Jan.1986.

Locality 9: Willows Stream area.

Site 1: east of fault in small stream, G.R.S48/661093.

Bed 1: gritty lens below basalt.

Collection: I.L.Daniel, 7 Mar.1984.

Appendix 5

Occurrence of Plant Fossil Taxa from the middle Clarence valley.

* indicates provisional identification of a taxon.

? indicates uncertain identification of a taxon
in a particular bed.

Leafy liverworts: 120,311.

Thallose liverworts: 120,?121,212,?330,615,711.

Phyllopteroides sp.cf.*P.dentata* Medwell: 410,411,412.

P.sp. cf.*P.lanceolata* (Walkom) Medwell: 411.

*P.sp.*cf.*P.laevis* Cantrill and Webb: 214,220.

*P.sp.*cf.*serrata* Cantrill and Webb: ?742,750.

Cladophlebis cf.*albertsi* (Dunker) Seward: 300.

C.australis (Morris) Halle*: 100,120,121,123,212,214,
217,220,310,321,330,410,411,412,521,522,523,
613,700,712,732,740,742,750,751.

C.prisca (Ettingshausen) McQueen*: 100.

Coniopteris ?*lobata* (Oldham) McQueen*: 100,210,300,
321,711,732.

Sphenopteris mackayi McQueen*: 310,700,?712,732,750.

Equisetum sp.: ?410,611,615,712,732.

Taeniopteris arctica Heer*: 412.

Thinnfeldia sp. cf.*T.chunakalensis* Sah & Dev*: 120,212,214,216,
217,220,300,330,521,522,740,?742.

"Linearphyll" (?*Ephedra**) 210,214,217,220,330,410,522,613,
700,712,732,742.

Podocarps *: 100,120,121,123,210,212,215,217,300,310,321,
330,410,411,412,521,522,523,614,700,711,712,718,740,
742,750

Agathis clarencianum sp.nov.: 012,100,120,123,210,212,214,
215,217,220,300,310,321,322,330,410,411,412,
521,522,523,610,612,613,614,620,700,701,711,
712,718,732,740,742,750,751.

A.seymouricum sp.nov.: 123,522,700,711,712,750.

- Araucaria danai* Ettingshausen*: 310,322,330,522.
- A.sp.sect.Columbea* * 212,220,
- A.sp.sect.Eutacta* *: 212,330,410,522.
- Ginkgo cuneiformis* sp.nov.: 111,120,121,210,215,217,220,
300,310,311,322,330,410,522,613,614,712,718.
- Nilssonia elegans* Arber: 100,121,123,220,330,732.
- N.pseudocompta* sp.nov.: 100,121,123,
- Taeniopteris stipulata* Hector ex McQueen: 100,212,214,?215,
?220,300,310,330,410,411,412,521,?613,?614,700,712,
?718,732,740,742,?750
- Nilssoniopteris* sp.: 100,122,?212,330.
- Anomozamites blechnoides* sp.nov.: 712,742.
- Otozamites* sp.: 421.
- Pterophyllum rectipinnatum* sp.nov.: 120,121,122,123,330,
?410,700,712,718,740,742,751.
- P.sp.A*: 100,742,751.
- P.sp.B*: 100.
- P.sp.C* cf.*P.clarencianum* McQueen: 100,120,214,330,740,742.
- Ptilophyllum seymouricum* McQueen: 212,310,522.
- Williamsonia valdensis* Edwards*: 100,330,522,?742.
- Araucariacean Cone scales and seed scales: 100,120,121,123,
310,330,522,613,614,712,?732,750.
- Ficoidophyllum ellipticum* sp.nov.: 100,123,310.
- F.attenuatum* sp.nov.: 100,121,?123,330.
- F.caperatum* sp.nov.: 100,123,?330,522,613.
- F.cuneatum* sp.nov.: 100,123,310,522.
- F.oligodon* sp.nov.: 212,214,220,330,412,522,742.
- F.ovatum* sp.nov.: 100.
- F.recurvum* sp.nov.: ?100,330,?412,522,742.
- Latifolium parvilobum* sp.nov.: all beds ^{containing dicotyledonous leaves} except 214,613,911.
- L.acutum* sp.nov.: 214,220,330,?410,411,412,613,718.
- L.crenatum* sp.nov.: 214,220,330,521,522,613,732.
- L.serratum* sp.nov.: 120,121.
- Lauroidophyllum cryptocaroides* sp.nov.: 100,212,214,217,330,
522,613,700,711,712.
- L.cinnamomoides* sp.nov.: 123,330,522,712,732.
- Liriophyllites parvisinus* sp.nov.: 214,220.

Parvifolium asymmetricum sp.nov.: ?100,123,212,214,
?300,522,613.

P.crenatum sp.nov.: 100,120,123.

P.emarginatum sp.nov.: 100.

P.membranaceum sp.nov.: 100,?123,?212,330.

P.obovatum sp.nov.: ?120,310,412,522.

Proteaceophyllum irregulare sp.nov.: 100,120,212,310,330,
521,522,613,750.

P.lanceatum sp.nov.: 410.

P.oblongum sp.nov.: 411.

Archaeopetala apiculatum sp.nov.: 522.

Carpolithus sp.: 100,120,121,217,220,522,613,615,?712.

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ADDENDA

p.4

In describing the sedimentary facies formed in sandy fluvial systems, R.G.Walker and D.J.Cant, 1979 (Facies Models, Geoscience Canada, Reprint Series 1, p.24)_state "During rising flood stage, the levees can be breached, causing the formation of a "crevasse splay" - a wedge of sediment suddenly washed into the flood basin, and commonly containing some of the coarse bedload portion of the river sediment". The sandstone lenses present in the otherwise muddy, coaly sediments at East Quail Flat, Alexander McKay Terrace and Horse Flat correspond closely to their description in having "a sharp base, overall graded bedding, and a sequence of sedimentary structures indicative of decreasing flow during deposition"(op.cit.).

p.6

Further discussion of stratigraphical correlations and the age of the deposits will be found in Reay 1980, and in a N.Z.Geol.Surv.Bulletin in preparation by M.B.Reay.

p.11

The fossils usually split with approximately equal amounts of anthracolemma on part and counterpart.

p.14

Treatment with alkali as per standard maceration procedures led to disintegration of delicate cuticles. Only well preserved specimens of *Agathis* and *Ginkgo* gave coherent cuticle after such treatment.

p.37

A stoma is an opening (also called the stomatal pore or aperture) in the epidermis of leaves and stems bordered by two guard cells. "It is convenient to apply the term stoma to the entire unit, the pore and the two guard cells" (K.Esau, 1977. Anatomy of Seed Plants, Wiley & Sons, New York, p.88. See also Stace, 1965.). The stomatal complex (also called the stomatal apparatus) consists of a stoma, two guard cells and associated epidermal cells (called subsidiary or accessory cells) that may be ontogenetically and/or physiologically related to the guard cells.

In this thesis, "stoma" is used in diagnoses and descriptions in the commonly accepted sense i.e. including opening and guard cells. In general discussion, it is used in the wider sense which is more properly termed the stomatal complex (as in "paracytic stomata" e.g. by C.R.Hill, 1986, p.124 in Systematics and Taxonomic Approaches in Palaeobotany, eds.R.A.Spicer and B.A.Thomas, Systematics Assoc.Spec.Vol.No.31).

p.44

"Cycadophyte" is here used as a general term for a taxon belonging to Cycadales or to Bennettitales but not attributable to either until cuticle studies establishes the order to which it belongs.

p.201

The figures of fossil leaves from earlier publications presented here (Appendix Figures 1 - 3, Vol.2, p.38 - 40) were hand drawn from the relevant publications for the purpose of convenient reference. It is acknowledged they may repeat the copying mistakes for which other authors are here criticized.